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HAPLOID AND DIPLOID GENERATIONS¹

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IT is eighty-five years since Hofmeister disclosed the existence of a basic similarity of life cycles as between the three divisions of land plants—bryophytes, pteridophytes and seed plants. The central feature common to these groups he designated an “alternation of generations,” appropriating a term that had been applied to conditions of very different nature in various animals, then to the succession of vegetative and floral shoots in seed plants. The heterogeneity of phenomena in animals and plants that were long grouped together as instances of an alternation of generations appears from the tabulation of *Zeugungskreise* in Haeckel’s “*Generelle Morphologie*.” Now by general consent, at least among botanists, the expression is limited to the type of cycle outlined by Hofmeister.

Another chapter began with discoveries announced by Overton in 1893. On the basis of these, and of observations by himself and by Guignard, Strasburger in the next year formulated the generalization that in plants of the three higher divisions an alternation in chromosome numbers coincides with the alternation of gamete-producing and spore-producing generations.

With the aid of this generalization, and of what has been learned more recently regarding meiosis in algae

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and fungi, it is now clear that a large proportion of species, distributed throughout most of the divisions and classes of the plant kingdom, display the regular alternation of a haploid, usually gamete-producing, with a diploid, usually spore-producing, generation.

Even when limited to this type of succession, the expression "alternation of generations" is not wholly satisfactory. A plant arising either from a zygote or from a spore may, through buds or runners or even spores of an additional type, give rise to an independent plant exactly like itself cytologically and genetically; each member of such a series in a very natural use of the word constitutes a generation. Hence the *generation* extending from zygote to spore or from spore to gametes may consist of a series of *generations* of subordinate order. Furthermore, each generation, in either of these senses, may include hundreds or thousands of *cell generations*. A more adequate expression, however, is lacking for the two alternating arcs of the life cycle, one diploid and closing with meiosis; the other haploid and ending in the production and union of gametes. In what follows, each of these major arcs will be called a *generation*, however many successive independent individuals it may include.

While characteristically one generation is haploid and produces gametes, the other is diploid and produces spores, this, like most broad statements, sometimes fails to hold. The possibility of the production of spores by the haploid generation has been noted; indeed, as in some of the rusts, a variety of spore types may appear, some borne by the haplont, some by the diplont. Other departures from the ordinary story result in the complete disappearance of spores (in any ordinary sense) from the cycle; others confuse or obliterate the cytological distinction between generations. Nevertheless, it is true that an alternation of a haploid, gamete-producing with a diploid, spore-producing generation is so wide-spread as to be a basic feature in plant morphology. Not less striking is the fact that such an alternation is quite unknown in animals.

Hofmeister's delineation was necessarily purely descriptive. But the appearance a few years later of the "Origin of Species" made it inevitable that the alternation of generations like other biological phenomena should be considered from a phylogenetic standpoint. The explanations that have been offered for the origin of this sequence fall into two classes: one commonly referred to as the theory of *homologous alternation*, for which Bower proposes the more satisfactory name of *transformation theory*; the other, the conception of an *antithetic alternation*, which Bower would call the *interpolation theory*.

The transformation theory, due originally to Pringsheim, supported in more modern form by Lang and Lignier among others, has remained somewhat nebulous. Originally it implied that the ability of a single plant to form either gametes or spores, as is the case in many algae and fungi, became differentiated as between distinct plants, and that the separate gamete-bearing and spore-bearing plants fitted themselves in time into a regularly alternating cycle. This conception seems not to have been clearly restated in terms of the cytological alternation; although there have been suggestions that the latter may have been arrived at by some such shifting or adjustment of the time of meiosis as would make it coincide with the transition from sporophyte to gametophyte.

The interpolation theory, suggested first by Celakowsky, developed on a cytological basis by Strasburger, and particularly supported in a long series of studies by Bower, holds that the sporophyte is a generation of later origin than the gametophyte, interpolated between gametic union and meiosis. Some writers have suggested that an alternation of generations may have arisen by transformation in algae and fungi, whereas in land plants it came into being by a process of interpolation. Something like this was the view of Celakowsky, who first spoke of "homologous" and "antithetic" alternations; and the double possibility is recognized by Bower in his latest discussion of the problem.

The phylogenetic question may be approached by asking, first: What causal factors determine that in the course of the life, for example, of a fern, a zygote gives rise to a sporophyte, whereas a spore develops into a radically different gametophyte?

When the gametophyte proved to be regularly haploid, the sporophyte regularly diploid, the suggestion was natural that the differences between generations depend upon the differences in chromosome number. But this conception quickly proved untenable. Apospory, apogamy, parthenogenesis and related phenomena, induced in some instances by external stimuli, in others fixed as permanent modifications of the life cycle, demonstrate that the number of basic chromosome sets has nothing to do with the matter. A diploid cell of a moss sporophyte can by proliferation give rise to a gametophyte similar, except that it is diploid, to the ordinary gametophyte of the species. Conversely, the haploid (unfertilized) egg of a seed plant may develop into a sporophyte with all the conspicuous characters of an ordinary sporophyte save that it is haploid. In various cases gametophytes have appeared with one, two and up to 17 chromosome sets; and sporophytes with from one to 32 sets. From the many instances known of this general nature it must be concluded that, in a species characterized by a regular alternation of generations, any cell that can develop into a new plant can give rise to any set of characters, gametophytic or sporophytic, the potentiality for which is present in its genetic constitution. The regular development of a zygote into a sporophyte, therefore, is dependent upon its response to surrounding conditions; if these conditions were sufficiently like those which ordinarily surround a germinating spore, the zygote would produce a gametophyte rather than a sporophyte. Conversely, a spore, under appropriate conditions, would give rise to a sporophyte rather than to a gametophyte. Moreover, a development of such exceptional nature, occurring under unusual conditions, may, in consequence of a mutation affecting the nature of the response of the developing cell, become an established habit. Apospory—the develop-

ment of a gametophyte from a sporophytic cell—has been induced in several ferns; in other ferns, apospory is of regular occurrence.

In considering how an alternation of generations may have arisen, it must be recalled that originally, in organisms which had acquired the habit of gametic union, meiosis (chromosome reduction) occurred in the two nuclear divisions first following the union of gamete nuclei. This is the condition that still prevails in many of the more simple living green and red algae. In such a case the vegetative cycle of the plant, whether this cycle involves a series of independent cells or a colony of cells, is haploid; the only diploid cell in the whole history is the zygote. It follows that, as Strasburger suggested in 1894, the haploid generation is the primitive one; and that the diploid generation has been in some way interpolated between gametic union and meiosis. To this extent the interpolation theory must be accepted.

It is not difficult to conceive how, in a lowly plant like *Volvox*, *Ulothrix* or *Oedogonium*, the interpolation in question might have occurred. In such a plant the four cells derived from a zygote and containing the nuclei resulting from meiosis regularly function, or may function, as starting-points of a new haploid generation—that is, as spores. But the zygote before meiosis possesses, so far as its chromosome complement is concerned, the possibility of development into a new plant (or colony). The only kind of plant into which the zygote can develop is one like that which produced the gametes; no potentiality is present for any other type of development. Remembering also that, at the level of development in question, any cell may give rise to a new plant, it can not be questioned that the same possibility is open to the zygote. Under usual conditions this does not occur; instead, meiosis intervenes. But under the influence of appropriate stimuli the zygote might develop directly into a diploid plant differing externally from the haploid parent only in the size differences possibly consequent upon a doubling of the chromosome complement. Precisely such a development of a diplont from a zygote has been observed by Mainx in

Oedogonium under conditions unfavorable to the occurrence of meiosis.

A procedure of this nature under special circumstances implies nothing of immediate evolutionary significance. But if a mutation were to occur affecting the response of the zygote to external conditions, a behavior otherwise exceptional might become the rule. In this way a genetic change involving the development of no new potentialities would bring about the production of a diploid following upon a haploid generation—the essential feature of an alternation of generations.

The new diploid plant may, as apparently it does in *Oedogonium*, itself form gametangia and diploid gametes. The union of these, if it occurs, will produce a tetraploid zygote. A repetition of this history, so far as repetition is possible, may result in a polyploid series of related forms. It can hardly lead to any other permanent consequence. But it is equally conceivable that, the production of a diploid plant being hereditarily fixed, this new plant may produce a cell or organ similar to a gametangium, whose nucleus or nuclei will undergo the delayed meiotic process. Now haploid cells (spores) are present capable of producing haploid plants; these produce gametes, and so on through the newly fixed cycle. A regular alternation of generations is established, in consequence of a single relatively slight mutation, by a diploid *duplication* of the haploid generation. The two generations are at this stage alike in structure ("homologous" in Celakowsky's sense).

The suggestion of such an origin of alternation is not so rash as a few years ago it would have appeared. For several green algae—species of *Ulva*, *Enteromorpha*, *Cladophora* and *Chaetomorpha*—are now known to present an alternation of just the sort that would be expected from an origin of this nature. Not only are haploid and diploid plants alike save for the reproductive cells that they bear, but the spore-forming organs (or cells) of the diplont are precisely similar to the gamete-producing structures of the haplont.

After the establishment of a diploid generation, it is to be expected that the evolution of gametangia and sporangia, now distinct, will proceed in different paths. Such differentiation of reproductive organs is illustrated in the brown algae *Ectocarpus* and *Dictyota*, the vegetative structures of haplont and diplont in each case being still indistinguishable. However, a general similarity between gametangia and sporangia long persists in many lines—as was long ago noted by Pringsheim. He considered likenesses between organs of these two types as evidences of "homology." The likenesses can now be explained as the expression of like genetic possibilities in the two generations; possibilities which, however, after the establishment of an alternation were modified by mutation in divergent directions.

The advantages resulting from alternation are at least two: First, it provides for the production of many spores, so increasing the possibilities of reproduction. But this end may be attained in other ways. The more important advantage is that emphasized by Svedelius. If a zygote nucleus undergoes meiosis, it can give rise in consequence of new groupings of chromosomes and chromosome parts to at most four genetically different lines. But if meiosis, delayed, occurs in many diploid cells descended from the same zygote, many or all of the possible new combinations of chromosomes and chromosome parts may be realized. The postponement of meiosis greatly increases, therefore, the possible range of variation.

Another possibility suggests itself. The major evolutionary advantage obtained by a postponement of meiosis would persist if the haploid generation were to disappear. The haploid spores resulting from meiosis, possessing all the potentialities of the species, should be capable, under appropriate conditions, of functioning as gametes. A mutation modifying in the right direction their response to ordinary conditions will lead them to behave regularly as gametes. Their union gives rise to a diploid zygote, this to a diploid generation, and this by meiosis again to

haploid gametes. Haploidy, except for the gametes, has disappeared in consequence of a second mutation.

In one species of *Cladophora* a mutation of just this nature seems to have occurred. Whereas other species of the genus so far investigated have an alternation of externally similar generations, *C. glomerata* has only a diploid generation, meiosis resulting in the production of gametes. There are indications of a similar history in certain races of *Ectocarpus*. This condition of diploidy exclusive except for the gametes appears also in at least one of the two orders of diatoms and, as well known, in the metazoa and in some protozoa.

In most plant lines, however, both generations have persisted. The generations being distinct and hence subject to more or less diverse environmental demands, differences between them naturally increase. Differentiation is likely to appear first, as in the cases cited, between their respective reproductive organs—gametangia and sporangia. Later, in some lines, have come differentiation in vegetative structure and differences in size and complexity. The advantage which inheres in the very existence of a diploid generation—that of a greater possible range of variation—is enhanced with any increase in the size and life span of the diplont, making possible meiosis and spore-production on a larger scale. It is, then, not surprising that selection has favored elaboration of the diplont. The haplont is reduced, at least comparatively; in the later stages of the differential evolution, certainly, it suffers an actual diminution.

Steps in the gradual dominance of diplont over haplont are illustrated in the orders of brown algae typified by *Laminaria* and *Fucus*. In *Laminaria* the diplont is large, often perennial; the haplont is a distinct but very small plant. In *Fucus* the haplont, no longer independent, has almost disappeared, being represented in the female line by but one cell generation preceding the gametes; in the male by three or four cell generations. Among the coenocytic green algae, approximately the same stage of reduction of the haplont as in *Fucus* appears in *Acetabularia*.

and *Bryopsis*; and in *Codium* the haplont has disappeared, gamete nuclei now being produced by meiotic divisions. In *Codium*, then, a life cycle like that in animals, wholly diploid save for the gametes, seems to have been brought about by a gradual reduction of the haplont; not, as apparently in *Cladophora glomerata*, by its sudden elimination.

A somewhat different method of origin of alternation is suggested by the conditions among red algae. The simpler members of this group, such as *Nemalion*, have developed a haploid post-zygotic phase. This phase, while distinct, is more or less dependent upon the gamete-bearing plant, to which it in turn gives rise through carpospores. It increases the possibilities of multiplication, because through it a single zygote gives rise fairly quickly to many spores. If, in such a plant, the zygote were to divide without meiosis, its development would most naturally be into a structure like that which previously arose from a haploid derivative of the zygote. If in the formation of carpospores by this now diploid structure the delayed meiosis occurs, the resultant spores will develop into a haploid gamete-bearing plant. The time of meiosis has been in effect shifted—a possibility already urged by Svedelius and Fritsch; the carpospore-bearing phase has been transferred from the haploid to a new diploid generation. The two generations are unlike ("antithetic") from the start.

A life cycle of the sort here postulated is actually known in two living red algae, a *Phyllophora* and a *Gymnogongrus*; it is probable in a *Liogora* and is suspected in other species. To pass from this condition to that seen in the majority of present-day red algae, an additional step is necessary—namely, the omission of meiosis in the development of carpospores; these now give rise to a diploid plant similar to that which bore gametes, and this plant produces spores (tetraspores) by meiosis.

These two steps—the transfer of a post-zygotic phase to the diplont and the duplication by the diplont of the longer pre-zygotic portion of the haploid cycle—could

conceivably result from a single mutation. In such case, the condition in *Phyllophora* and *Gymnogongrus* would represent a reduction of the diplont, as some, indeed, consider it to be. But whether the new developments proceeded by one step or by two, the more extensive life cycle here, as in the cases previously discussed, has resulted from the expression by a diploid zygote of genetic possibilities already developed by a haploid generation. This is the basically single method by which an alternation of generations seems to have arisen in green, brown and red algae, as well as in fungi—or their algal ancestors.

The sporophytic evolutionary sequence in bryophytes is most commonly traced from the condition in *Riccia*, whose diplont is but a group of spores surrounded by a layer of sterile cells, to that in *Anthoceros* and mosses, in which the diplont, though still dependent, is an elongated structure with a considerable proportion of differentiated vegetative (non-spore-bearing) tissues. It is upon such a seriation that the interpolation theory of Strasburger and Bower has rested. As commonly understood, this theory implies that the sporophyte began by the division of the zygote nucleus without meiosis, one, two or a few cell generations so interpolated constituting a rudimentary sporophyte.

While the gradual development of a diploid generation in this manner is conceivable, the facts of alternation in the algae suggest caution. It appears from these that if a zygote is to divide, retaining a diploid chromosome complement, it must grow into a structure similar to one already produced by the haploid generation. Something resembling the diplont of *Riccia* would be thus produced if the haplont had previously developed a post-zygotic spore-producing phase. Such a phase has been seen in the haploid red algae; it is known also in one green alga, the much-discussed *Coleochaete*. If, in an organism with a post-zygotic haploid phase similar to that of *Coleochaete*, the zygote were to divide without meiosis, the natural consequence would be a transfer of the post-zygotic phase from haplont to diplont. Meiosis would be delayed until

spore-formation. The two generations would be unlike, as they are throughout the bryophytes. Members of this division have not, like the more complex red algae, taken the further step of duplication of the gamete-bearing plant.

It is true that some morphologists, particularly Goebel, have considered the bryophytes to represent a descending series, derived possibly from an algal ancestor whose two generations were similar. This view implies a progressive reduction of the diplont to a minute parasitic structure, contrary to the tendencies widely manifested in other classes. To support the possibility of a reduction of the diplont, the conditions in such red algae as *Phyllophora* and *Gymnogongrus* have been cited. But these, it has been shown, are capable of a very different interpretation. The only other suggested analogy is found in *Cutleria multifida*, whose diplont is in general smaller than the haplont. However, there is evidence that either generation may vary to some extent toward the character of the other; moreover, the ordinary diplont of *C. multifida* resembles the haplont of *C. adspersa*, and even more closely both haplont and diplont of the related *Zanardinia*. The complex of genetic possibilities in this order awaits further study. In the absence of any conclusive case of diplontic reduction, the most plausible conception as to the ancestry of bryophytes is that of an origin of alternation by transfer, followed by a gradual elaboration of the diplont.

Pteridophytes and seed plants undoubtedly present late stages in the increasing dominance of the diplont. In themselves they supply no evidence as to how their alternation originated. If pteridophytes derive from bryophytic ancestors, then alternation in the whole series from bryophytes to seed plants is explainable by a transfer of a post-zygotic phase followed by changes in the relations of the two generations similar to those that have occurred in many algae. If, on the other hand, pteridophytes arose independently, they may be traced back to algae which, like *Ulva* and *Dictyota*, possessed two similar generations, the diplont having arisen by duplication

of the haplont. The discovery of the Devonian Psilophytals, generally held to represent an ancestral condition of some or all pteridophytes, is not conclusive on this point. The Psilophytals are thought by some to evidence a direct algal descent for pteridophytes; by others to present a transitional stage in the evolution of pteridophytes from bryophytes.

The angiosperms in general possess an extremely reduced haplont comparable with that of *Fucus*. A few members of one family (Plumbaginaceae), if Dahlgren is correct, have reached in the female line essentially the condition of *Codium*, in which gamete nuclei are the immediate consequence of meiosis. The reduction series represented in the seed plants and the parallel series in algae, represented by *Laminaria*, *Fucus*, *Bryopsis* and *Codium*, show that a diploid condition like that in animals can result from reduction and final elimination of a haploid generation. The possibility that similar reduction and elimination occurred in the ancestry of the metazoa has been suggested from time to time. The serious objection to this suggestion is, of course, that no intermediate stages in such a history are offered by any known animals, fossil or living, whereas intermediate stages are the rule in living plants. It is easier to suppose that the diploid condition in animals arose very early in phylogenetic history by the means previously suggested—the sudden elimination of a haploid generation through the expression by the cells resulting from meiosis of their inherent gametic possibilities.

It may be concluded then that:

In an otherwise wholly haploid organism, the diploid zygote may, given special appropriate conditions, develop directly without meiosis into a new colony or multicellular individual. This possibility may in consequence of a single mutation become the regular behavior of the zygote under ordinary conditions. A diploid generation is then established.

The new diplont can display only characters already represented in the genetic constitution of the haplont. In

the simplest case, this implies a *duplication* by the diplont of the structure of the haplont. An alternation of generations seems to have arisen by duplication in green and brown algae; possibly also in the ancestors of pteridophytes and of seed plants.

If the haplont has developed a distinct post-zygotic phase leading to spore-formation, the newly established diplont displays the characters of this phase. The post-zygotic phase is *transferred* from haplont to diplont. The two generations are then unlike from the start. An origin of alternation by transfer seems to have occurred in the ancestry of bryophytes; and in that of pteridophytes and seed plants if these derive from bryophytic ancestors.

Alternation in long-cycled red algae apparently came about through both transfer and duplication.

Alternation being established, the general tendency is toward an elaboration of the diplont and a corresponding reduction of the haplont. Reduction has led, in *Codium* and apparently in the female line in a few angiosperms, to the complete elimination of the haplont save for the cell generation that includes the gametes. This is essentially the condition in animals.

But in one species of *Cladophora* and possibly in a race or races of *Ectocarpus* it appears that an elimination of the haplont has come about in a single step—the final cell products of the diplont by a mutation affecting their response to external conditions taking on the function of gametes. In view of the absence of intermediate stages, so abundant in plants, it is probable that in the ancestry of the metazoa the haploid generation was thus eliminated in one step rather than by a gradual process of reduction.²

² This paper having been prepared for oral presentation, literature citations were kept at a minimum. But to avoid seeming to claim too much of novelty, it should be mentioned that Lang, in 1909, argued for the equipotence of haploid and diploid cells as a basis for a theory of alternation. His further discussion, however, was on different lines from the present one. Fritsch's recent suggestion also should be noted, that an alternation such as appears in *Cladophora* "must have occurred by a sudden mutation."

SUPRA-SPECIFIC VARIATION IN NATURE AND IN CLASSIFICATION¹

FROM THE VIEW-POINT OF ZOOLOGY²

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DURING the last three years biologists of every field have shown renewed interest in problems of organic evolution. This is clearly the result of recent developments in genetics, taxonomy, paleontology and some other sciences which are basic to an understanding of species. Not many decades ago a symposium on evolution seemed to call for declarations of scientific creeds, on the basis of which biologists were split into rival schools and independent sciences. To-day we are more interested in collating and correlating sound data from all the fields which have anything to contribute.

In the wide range of living forms, there is more than one kind of species. Entirely aside from nomenclatorial difficulties, species differ in different groups; and even within single groups they vary with the age and the size of the population, the mutation rate, the recency of mutation, the chance for hybridization with related species and in still other ways. These factors are so diverse in different groups as to account for the different or even contradictory emphases placed by different investigators upon mutation, hybridization, polyploidy, sterility mechanisms, other isolating factors and selection in the evolution pro-

¹ Read at a symposium of the American Society of Naturalists in joint session with the American Society of Zoologists, the Botanical Society of America, the Genetics Society of America, the American Phytopathological Society and the Ecological Society of America. The American Association for the Advancement of Science, Atlantic City, N. J., December 30, 1936.

² Contribution from the Department of Zoology, Indiana University, No. 264 (Entomological Series No. 18). The detailed data, of which the present paper is a summary, are to be found in the author's 1930 and 1936 publications on *Cynips* (Ind. Univ. Studies 84-86, and Ind. Univ. Sci. Ser. 4). The last-named publication contains a more extended treatment of higher categories.

ess. But where observations are accurate and sufficient, they can be accepted as applicable to the material studied; and it can not be over-emphasized that there is no reason for expecting simple and uniform explanations of evolutionary processes among all kinds of organisms.

The picture which I shall present is based upon an intensive study of the gall wasp family Cynipidae and on only a more casual acquaintance with species in other groups. Whether this material is translatable to other portions of the living world must be determined through comparable studies of other organisms.

DEFINITION OF HIGHER CATEGORIES

Confusion will be avoided if we call the basic taxonomic unit the species. It is the unit beneath which there are in nature no subdivisions which maintain themselves for any length of time or over any large area. The unit is variously known among taxonomists as the species, sub-species, variety, Rasse or geographic race. It is the unit directly involved in the question of the origin of species, and the entity most often indicated by non-taxonomists when they refer to species. Systematists often introduce confusion into evolutionary discussions by applying the term to some category above the basic unit. Anything above this unit, even though it may be called a species, is, in reality, a higher category whose evolutionary history is essentially the same as the history of such other classificatory composites as are commonly called complexes, sub-genera, genera, etc. All categories above the basic taxonomic unit present a single problem, which is to determine the nature and the manner of origin of a group of units, in contrast to the nature and origin of the units themselves.

NATURE OF GENERIC CHARACTERS

A higher category is traditionally defined as a group of species with at least some characteristics which extend throughout the group. The opinion is current that the

morphologic or physiologic characters which define these categories are usually different from those which distinguish species. In those instances where the same characters are involved in specific and generic differentiation, it is currently understood that the differences between species are not as great as the differences between higher categories. Just as some of the geneticists have insisted that the laboratory genetics may explain the nature and origin of Mendelian races, but not of natural species, so others indicate that the qualities of higher categories must be explained on bases other than those involved in species.

On the contrary, recent taxonomic studies and such experimental analyses as have been made of natural species indicate that Mendelian genetics provides all the hereditary mechanism necessary for the evolution of species as well as for laboratory races; and I shall undertake to show that the same genetics is all that is involved in the origin and development of the characteristics of higher categories.

First, as to the constancy of generic characters: This should mean, genetically, that the genes which differentiate species are more liable to change than those which define genera. With many plant and animal groups, Miocene, Oligocene or older in origin, we are asked to think of generic characters as those which have undergone little or no mutation for twenty, thirty or even hundreds of millions of years. While the geneticists have shown that some genes are more mutable than others, laboratory data can hardly be counted on to prove that there are genes that remain unchanged for such long periods of time. The impression that there are such long-stable characters is, therefore, based primarily on the evidence of current classifications. But this is arguing in a circle. It proves nothing as to the stability of generic characters to exhibit genera that have been delimited by stable characters. It would be more important to know how many characters are stable throughout groups that are evolutionary units.

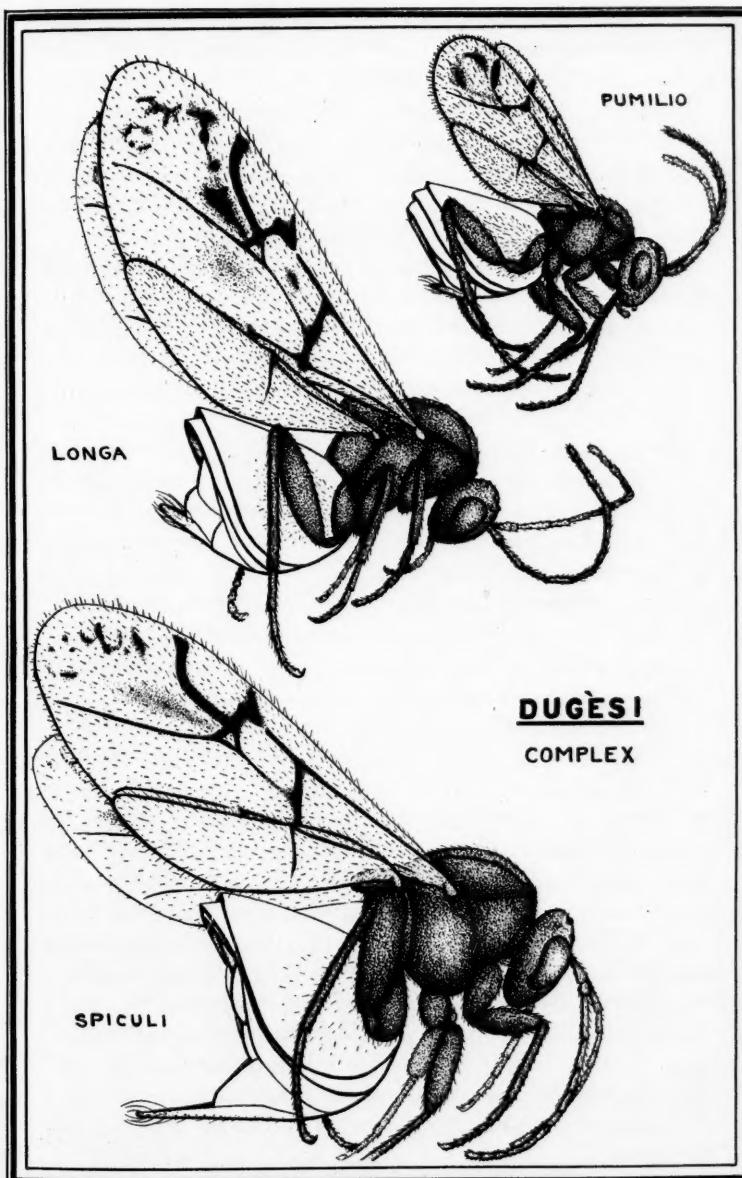


FIG. 1. THREE CLOSELY RELATED SPECIES

Mexican gall wasps. Note differences in wing length, abdominal spines, etc.
Major mutations obscure the really close relations of such species.

Too often classifications are built on a limited number of characters and relationships recognized by the sole criterion of similarity. Where only minor mutations have been involved, this leads to no difficulties, but where major mutations have occurred, closely related species may differ so radically as to obscure their relationships. It has been one of the major contributions of genetics to show that similarity is not wholly safe as a criterion for the recognition of relationships. In modern taxonomic studies we have many cases of closely related but dissimilar species which have hitherto been placed in apparently divergent groups. It is only when phylogenetic interpretations are based upon a variety of morphologic, physiologic and distributional data that true relationships in such instances become evident.

To illustrate from the gall wasp family Cynipidae, it is to be noted that the genera and higher groups in the accepted classifications have been defined for more than half a century by remarkable differences in wing length, relative proportions in thoracic and abdominal structures, antennal segmentation, body sculpture and clothing and other clear-cut characteristics. The book-classification furnishes a typical or even extreme example of higher categories discretely defined by stable characters. And yet if the genera of this family are rearranged on modern phylogenetic bases, the stability of the generic characters proves to be quite illusory and the instability of practically all characters the rule. So-called genera that have been delimited by peculiar and constant wing lengths, distinctive thoracic or abdominal structures, etc., prove to be artificial aggregations of species that are phylogenetically remote. A phylogenetic classification gives genera which are difficult to define because none of the characters is fixed throughout the species that must be recognized as related. In *Cynips*, there are nearly a hundred characters which are available for classificatory purposes, but not a single one of these extends uniformly throughout the genus.

Whether the Cynipidae are a fair sample of other organisms must be determined by more studies than we yet have. That there is evidence of the same variability of the characters in other groups is strikingly attested by the wide-spread tendency in present-day systematics to multiply the number of genera at the expense of the size of the groups. Such small or monophyletic genera as are commonly recognized by vertebrate taxonomists, and notably by the ichthyologists, merely evidence the unwarranted faith which systematists have in the stability of characters as generic criteria and their hesitancy to believe that major mutations may occur among vertebrates as well as among fruit flies. If the stability of generic characters can be demonstrated only by limiting genera to a few or to single species, we are in reality establishing the fact that there are few if any characters which are stable through any long time or through any large series of units.

From the foregoing it may be concluded that exactly the same characters differentiate Mendelian races, species and the best-defined genera. The accompanying table shows that this is what we do find when we make modern phylogenetic interpretations, instead of depending on such traditional arrangements as are current in elementary keys and catalogues. In genetic terms, this means that mutations developing within the heart of a population and not prevented by some sort of isolation factor from interbreeding with the parental stock bring about an extension of the individual variation within the species. If, on the other hand, the very same mutation, large or small, is isolated or selected from out of the parental stock, the new species which ensues is differentiated by the same characters which were the basis of the Mendelian race in the first instance. But, finally, if the specific differentiation involves major mutations which are continued through any series of species, we ordinarily consider that two genera have evolved. Since exactly the same characters are concerned in all these cases, there is no need for believing

CATEGORICAL SIGNIFICANCE OF CHARACTERS IN CYNIPIDAE

Characters	Genera e.g.	Diagnostic for:	
		Species within complexes e.g.	Individuals within species e.g.
EYES: protrusion	Disholcaspis	X. volutel.	B. eburnea
ANTENNAE: no. of segm.	Cynips	X. crystal.	
THORAX			
Size: proportions	Disholcaspis	C. villosa	C. anceps
Pronotum: dors. width	Aulacidea	Philonix	Philonix
Paraps. groove: length	Besbiceus	C. weldi	B. eburnea
Mesopleuron: sculpt.	Xystoteras		
Fov. groove: subdivis.	Diplobius		
Sculpture, clothing	Disholcaspis	X. crystal.	C. fulvic.
ABDOMEN		X. crystal.	
Size: proportions	Disholcaspis	C. villosa	B. eburnea
Shape	Heteroecus	X. crystal.	B. eburnea
Segments: rel. sizes	Heteroecus	Philonix	B. eburnea
Pubescence: extent	Disholcaspis	C. villosa	Acraspis
HYPOPYGIAL SPINE	Disholcaspis	C. villosa	C. bulla
WINGS			
Length: 0.10-2.00	Besbiceus	Acraspis	B. eburnea
Radial cell: closure	Cynips	Lytorhod.	C. pictor
Venation	Feron	C. mellea	C. pictor
TARSAL CLAWS: toothing	Disholcaspis	C. mellea	C. mellea
GALL			
Location: on plant	Cynips	C. aggreg.	Neur. pacif.
Larval cells: number	Cynips	Acraspis	C. cruenta
Tissues involved	Atrusca	C. arida	
Separability	Cynips	Diastroph.	Liposthenes
Special covering	Atrusca	Acraspis	C. erinacei
HOST: restriction			
To single species	Heteroecus	C. dugesi	C. unica
To related species	Cynips	C. bulboid.	C. incompta
LIFE HISTORIES			
Larval life: duration	Amphibolips	D. pernic.	C. fulvic.
Season of emergence	Disholcaspis	C. dugesi	C. sierrae
Sex ratios	Aulacidea	Diplolepis	D. rosae
Heterogeny	Aulacidea		

that different mechanisms of heredity are at the base of the evolution of different categories.

THE ORIGIN OF HIGHER CATEGORIES

In the course of evolution, old species are related to the new as links in a chain. It is unfortunate that the classic analogy should have been with a tree, for the picture is that of an infrequently dividing chain. Minor mutations in a few characters are the usual bases by which one link differs from the next; major mutations occasionally occur; but nowhere in the genetic, taxonomic or paleontologic data is there sound justification for believing that great changes in whole groups of characters are the sources of the higher categories.

The phylogenetic trees which substantiate the major catastrophe idea are most tree-like when the fewest fossil

or existent species are at hand to limit the imagination of the artist. The known species are too often united by dotted extensions of the lines representing the existent data. An experienced paleontologist or taxonomist should be able to take the sticks from any woodpile, no matter how diverse their origin, and unite them so skilfully that they will not only look like a tree, but pass among biolo-

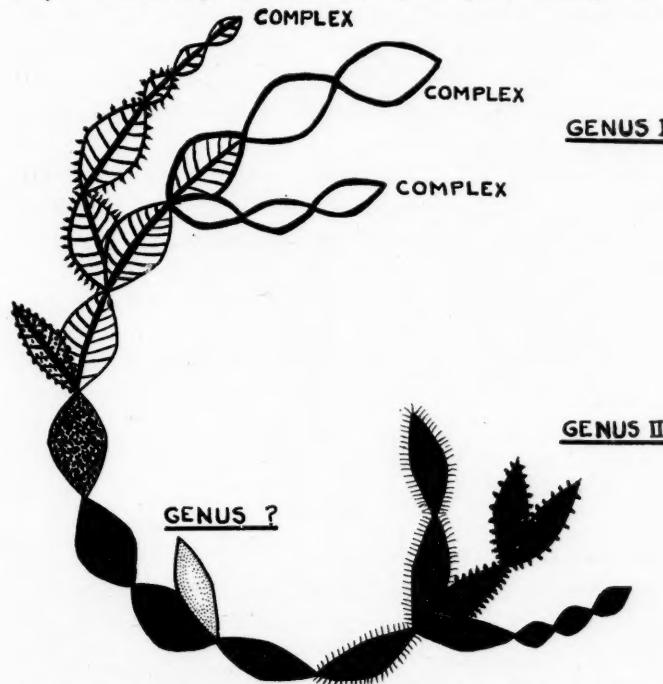


FIG. 2. THE EVOLUTIONARY PATTERN IS THAT OF A CHAIN
There is no discontinuity in such a chain, although the diverse ends may represent different genera.

gists as derivatives of the root system of a single dicotyledonous plant. The only restriction is that no species, living or fossil, shall be derived from any other known species, although both, according to the traditional rules, may be derived from a hypothetical "common ancestor." Such a procedure has the merit of putting embarrassing

questions far enough into the background to allow us to ignore them when we wish. But if we rub out the dotted lines and hypothetic connections from these phylogenetic trees, what do we know about the origin of higher categories?

We know, first of all, that there is an increasing list of fossil connecting links between groups that subsequently became the present-day genera, families, orders, etc. The paleontologists are contributing an increasing number of such cases. And connecting links spell continuity in the organic chain, not discontinuities "dependent on Lamarckian effects of great geologic upheavals," as the older paleontologists would have had it. Because of the difficulty of recognizing close relationships where major mutations have occurred, the paleontologic chains are probably more continuous than is yet realized.

Beyond the fossil record, we have the evidence of existent species as to the nature and origin of higher categories. Such data are in reality more complete than the fossil record both in the number of known species and in the availability of the characters by means of which relationships may be interpreted. It may fairly be objected that the present-day picture shows nothing but the end products of histories that are often very ancient. It is true that living populations do not have exactly the same constitutions as when they were first isolated from their parental types. In the course of the hundreds of thousands or millions of years during which each population has been in existence, intra-specific mutations have extended the range of variation, hybridization with related species may have introduced new allelomorphic genes, and chance elimination or selection may have dropped some factors out of the inheritance of the group. The complete picture in any case should show a third dimension representing intra-specific evolution; but it is only when a detailed fossil record is available that the vertical can be correlated with the horizontal evolution of a group.

Meanwhile the present-day species tell so much of the story that it is surprising that they have not more often been called upon in studying the history of evolution. The neglect of these data is very largely due to the pre-occupation of taxonomists with local faunas and floras. Among plant and animal groups of any size, there are hardly twenty which have had the monographic treatment necessary for an understanding of the relationships of higher categories. European studies rarely get out of Central Europe, though the evolutionary histories of those

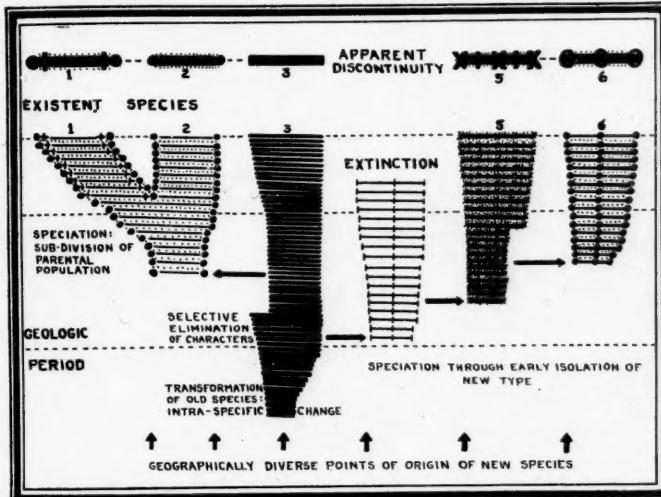


FIG. 3. THE ORIGIN OF EXISTENT CHAINS

Present-day species represent cross-sections of fluctuating populations which originated at different times and in different places.

forms must be followed through Mediterranean, North African and Asiatic groups if one is to find the links between complexes and genera. American studies too often stop at international boundaries. In consequence, it is concluded that American genera are sharply limited, discrete groups, although the pursuit of those same evolutionary lines into the north or into Mexico and Central America might lead to very different conclusions.

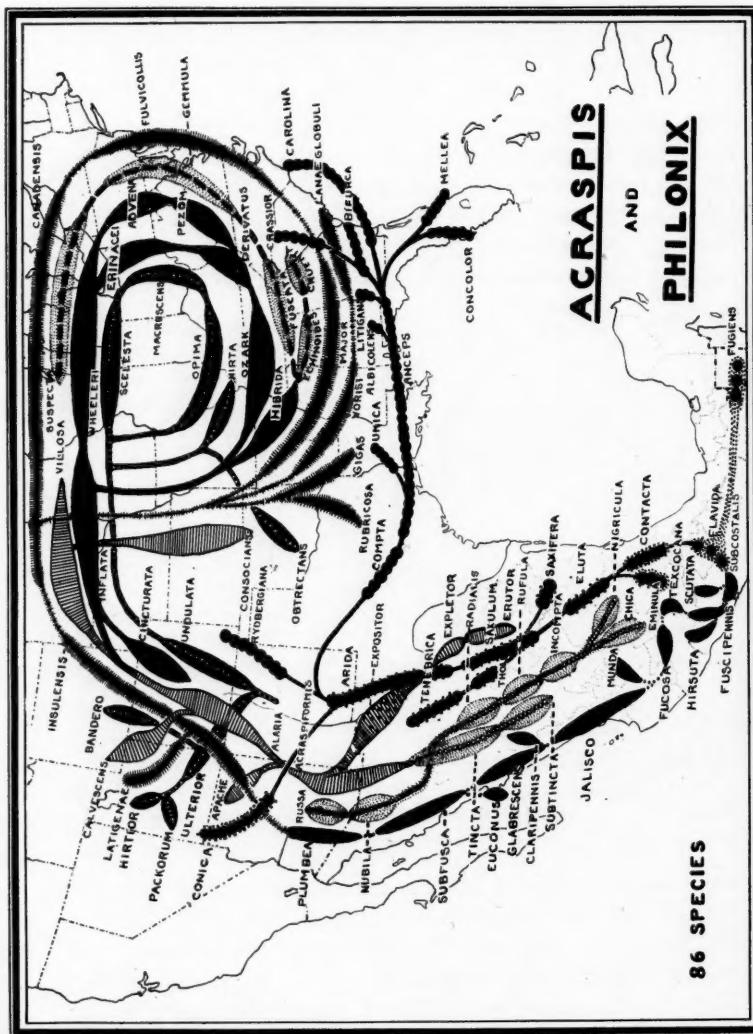


FIG. 4. A CHAIN OF EXISTENT SPECIES
Gall wasps of the *Caninae* group of genera. See Fig. 5.

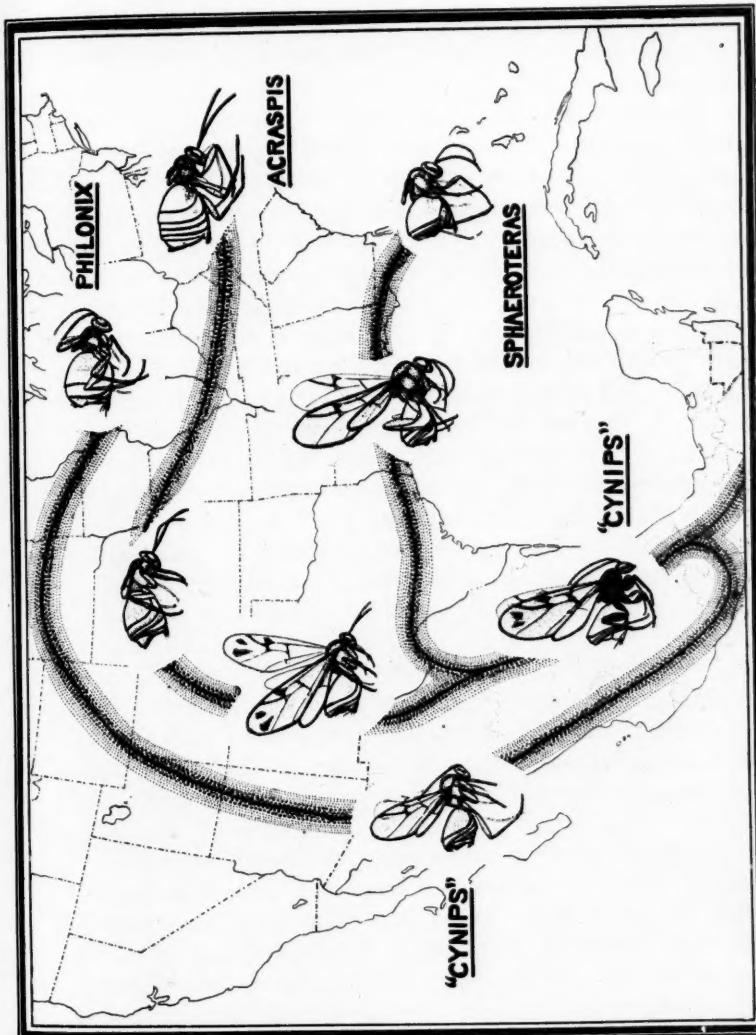


FIG. 5. EXTREME TYPES IN A CONTINUOUS CHAIN
See Fig. 4 for the 86 species involved. The diverse ends of this chain represent the distinct "genera" *Philonix*, *Acraspis*, *Sphaeroteras* and *Cynips*; but the limits of the genera are indefinable because of the continuity of the chain.

Illustrating again from the Cynipidae: In 1930 we knew 50 species assignable to the genera *Philonix*, *Sphaeroteras* and *Acraspis*. The groups were well defined, higher categories of long standing in the literature. With the existent species as links in the phylogenetic chains, the 9 complexes involved were traced back to Southern Arizona, where they all ended, still as distinct complexes in different genera. At the same time, studies of the American species of *Atrusca* similarly showed 4 unconnected lines leading to the same portion of the Southwest. I hypothesized ancient origins for the 13 groups somewhere in the Southwest or in northern Mexico, and even looked to the spectacular geologic history of that area for possible factors in the origin of the categories! But in 1931-32, and again in 1935-36, we carried on fieldwork over some 18,000 miles of Mexican and Central American back-country. The 70 new species which we discovered in those particular groups continued the American chains southward to points where many of them united. We can now put 44 of the species of *Atrusca* into one phylogenetically continuous chain, and the 86 species of the *Acraspis-Sphaeroteras-Philonix* group into another continuous chain.

As in the building of a jig-saw puzzle, too many missing pieces leave a phylogenetic picture uninterpretable; but there is no excuse for hypothesizing centers of origin and ancient connecting links for groups which have not been pursued to the limits of their present-day distribution.

The phylogenetic pictures which we have been building represent chains of existent species. Each is isolated from its closest relatives by geographic or other factors. Each is related to the next as the most closely related species in any complex—and yet the diverse ends of these chains represent distinct and diverse genera. Unpublished studies have already shown that five of the other genera in the family will be united in these same chains, via Mexican and Rocky Mountain material that we have

collected. Ultimately some four or five hundred species may fall into a continuous chain. Similar collapses of generic definitions are not unknown among other groups, but how many of the living forms of plants and animals may ultimately be placed on continuous chains, there is no way of predicting. That many of the connecting links are no longer in existence is evidenced by every fossil species which is different from a living form and by the present-day absence of whole groups from large areas (deserts, tropic lowlands or mountain divides) across which the original paths of migration must have extended. The higher the taxonomic category, the less, in general, is the chance of finding living connecting links; but for many complexes and genera the living record may be more detailed than that supplied by fossils.

In these chains there are no real discontinuities that may be taken as the limits of higher groups. Apparent discontinuities due to our lack of knowledge or to the actual extermination of once-existent forms may allow for some agreement among taxonomists as to the limitations of the higher groups; but such breaks in the data do not indicate real discontinuities in the history of the chain. While there are points at which particular characters show major mutations, these do not coincide with the points of major mutation in other characters; and phylogenetically sound classifications must be based on all the heritable characters that are taxonomically available. Without coincidence in the extent of the several characters, the limitation of a higher category appears to be an arbitrary procedure, no matter how diverse the ends of the chains may be. As matters of classificatory convenience, we shall undoubtedly continue to utilize higher categories; but in so doing we must recognize the artificial nature of their limitations.

Higher categories are, then, definable as arbitrarily delimited sections of phylogenetically continuous chains of species. They are not necessarily groups of similar species or groups of species with constant characters.

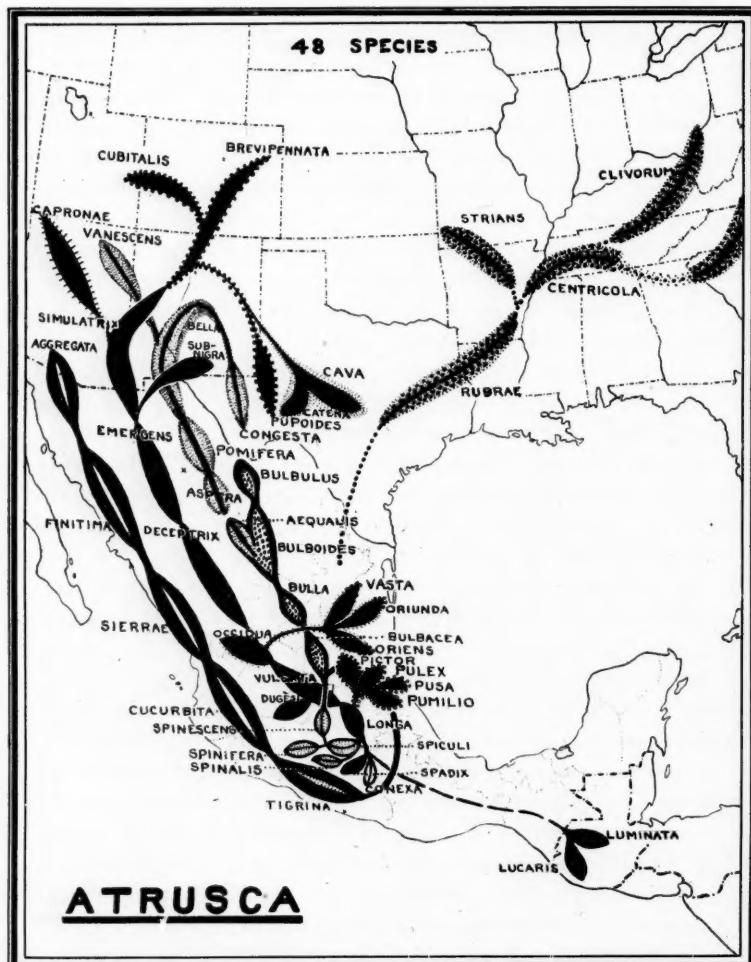


FIG. 6. ANOTHER CHAIN OF EXISTENT SPECIES

Previous to the discovery of the Mexican species, the ends of this chain appeared as well defined and not closely related complexes.

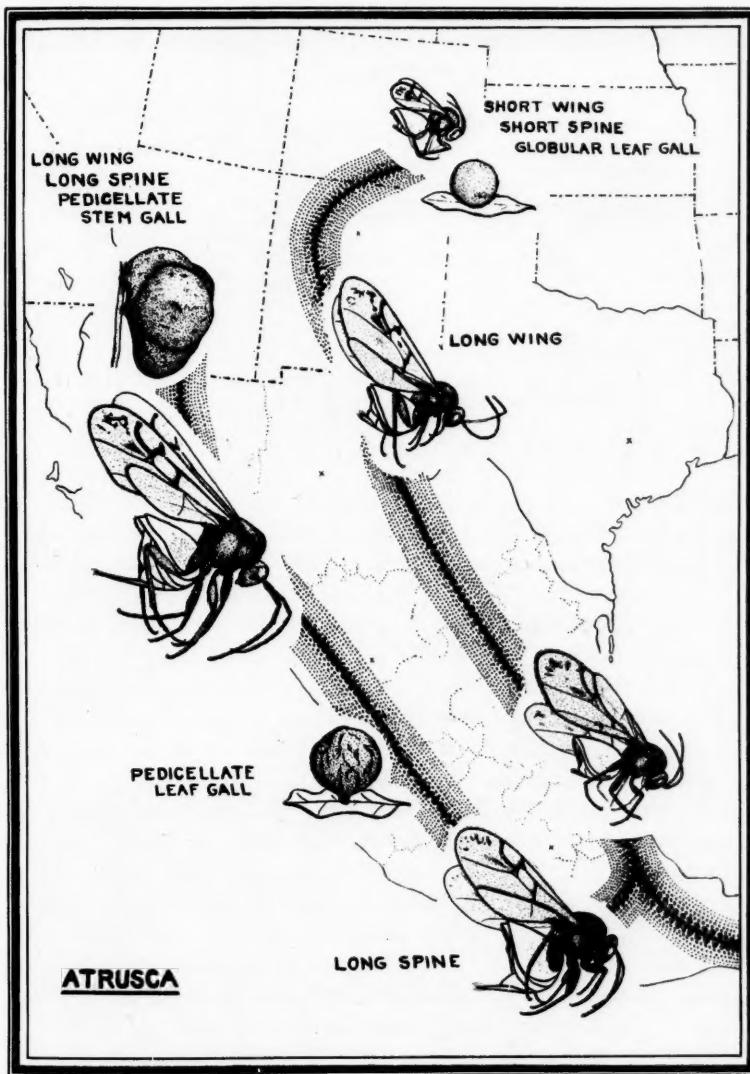


FIG. 7. EXTREME TYPES IN THE CHAIN

See Fig. 6 for all the species involved. Compare wing, abdominal spine, gall shape and location of galls in the extreme types. The major mutations in these several characters occurred at different points in the chain.

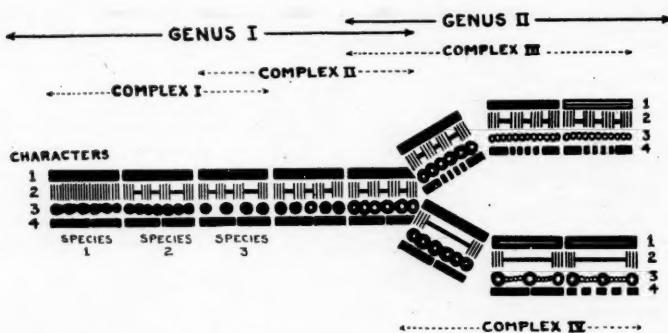


FIG. 8. THE ORIGIN OF "GENERIC CHARACTERS"

In such a chain, each character originates (by mutation) and disappears independently of the other characters of the species. There is no concomitant mutation in the several characters, although the extreme ends of such chains are the higher categories of taxonomic classifications.

They are not necessarily groups of species which have originated by radiate evolution from a common ancestor. But higher categories are series of phylogenetically related species. The same system of genetics which explains Mendelian races and the origin of species will explain the nature and origin of any higher category, for there are no characters in such categories apart from the characters of the species of which the group is composed. Evolution is never more than a process of change in single genes, rearrangements of gene complexes and aggregations of genes, and the modification of gene frequencies in the development of specific populations. There is, after all, no evolution apart from the modification of existent species or the differentiation of new species.

SUPRA-SPECIFIC VARIATION IN NATURE AND IN CLASSIFICATION

FROM THE VIEW-POINT OF BOTANY¹

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You are all familiar with the old story of the three blind men and the elephant. One felt of the trunk and said, "Ah, yes, an elephant is like a snake." Another felt of the ear: "Obviously your training is at fault; the animal is like a fan." While the third, having caught hold of the tail, said, "You are both fools. The elephant is like a rope." The story interests me because in one person I combine the viewpoints of all three of these gentlemen. Some ten years ago I thought it might be possible to make an easy synthesis of taxonomy and genetics by studying the minutiae of variation in a few species. When that was done, it seemed to me, one should be able to state quite definitely how evolution was actually proceeding. By painfully detailed methods I studied a few species of *Iris*, a few of *Aquilegia* and a few of *Tradescantia*. Now that the returns are beginning to come in I find that my hypothesis was partially correct. One can determine, one can even demonstrate, how evolution is proceeding in *Tradescantia* (Anderson, 1936b and 1936c), what it is doing in *Aquilegia* or what its effects are in the genus *Iris* (Anderson, 1936a). But Evolution in general, evolution with a big E, that is another matter. In the terms of the story I know that the snake and the rope and the fan are all there and that somehow they do fit together; but such a state of mind, while interesting, does not make for a comprehensive understanding of elephant morphology.

¹ Read at a symposium of the American Society of Naturalists in joint session with the American Society of Zoologists, the Botanical Society of America, the Genetics Society of America, the American Phytopathological Society and the Ecological Society of America. The American Association for the Advancement of Science, Atlantic City, N. J., December 30, 1936.

However, my confusion is excusable. By contrast with the higher animals, the flowering plants are extraordinarily varied in the details of their evolutionary processes (Anderson, 1931). The forces which isolate individuals and groups of individuals are tremendously diverse, sometimes even in closely related groups. One species may be self-sterile, though others in the same genus are almost continuously self-pollinated. Some plants are ephemeral creatures of one season and, like the higher animals, depend solely upon sexual reproduction. Others are potentially immortal and are capable of colonizing continents by vegetative reproduction alone. Several of the complicating factors which may occur among the flowering plants are never found among the higher animals. We must at least consider their existence before we can discuss the origin and relationships of higher categories in the flowering plants. Not until some of this preliminary brush has been cleared out of the way shall we be ready to consider the underlying ground plans.

By the way of example, therefore, I should like to consider *Amphidiploidy*, one of the most important of these special factors. While it has since been shown to occur in nature, the first clearly demonstrated case was that of a cultivated house-plant. *Primula kewensis* originated in England as a sterile hybrid between an Abyssinian species of *Primula* and one from Asia. It was attractive and winter-flowering and so in spite of its sexual sterility was propagated vegetatively. Eventually on several different occasions plants of this sterile hybrid gave rise to vigorous fertile branches, whose seed, in spite of the plant's hybrid origin, bred true to type. Cytological study provided a simple explanation of the phenomenon (Newton and Pellew, 1929). Each of the parent species had nine pairs of chromosomes. The sterile hybrid, as we would expect, had eighteen chromosomes, nine from each species, but they were too unlike to pair and form fertile gametes. The fertile branches, however, had just twice the number of chromosomes, 36 per cent. They had orig-

inated when a nuclear division had not been followed by a cell division and from the resulting giant cell there had grown out an amphidiploid branch with two full sets of chromosomes, that is, two of each of the parental species. It could, therefore, form germ cells in a substantially normal fashion and was fertile and true-breeding.

Amphidiploidy, the production of fertile, true-breeding hybrids by doubling of the chromosome number, is now known to be fairly wide-spread among the flowering plants, though certainly exceptional elsewhere. It has a number of important effects in so far as the problems we are discussing are concerned. In the first place, it makes

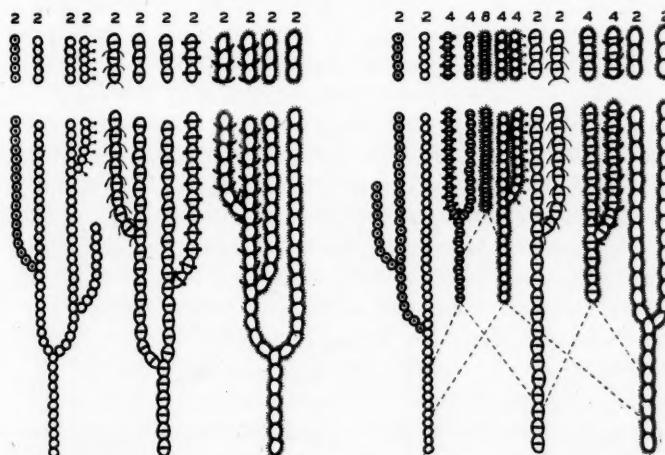


Diagram illustrating the effect of amphidiploidy upon phylogenetic relationships. The lower portion of the diagram illustrates the course of evolution in three related stocks, without amphidiploidy (left) and with amphidiploidy (right). The upper portion of the diagram represents the morphological relationships of the present-day species, the numbers at the top referring to the numbers of sets of chromosomes (2 indicates a diploid species or variety, 4 a tetraploid, etc.). The chief point of the diagram is to show that from mere inspection of the present-day species it is possible, in the absence of amphidiploidy (left), to hypothesize fairly exactly the course of evolution. In the presence of amphidiploidy (right) it is not possible to reconstruct the course of evolution from a mere analysis of present-day species. In as simple a case as the one diagrammed it would be possible from the morphological evidence *and* the chromosome numbers to reconstruct the phylogenetic history in a fairly accurate manner.

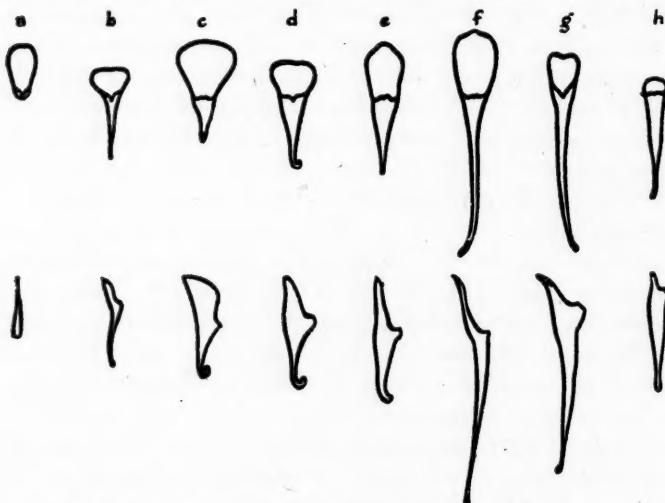
for morphological relationships which are reticular rather than dendritic, that is, a complex interwoven network instead of a tree or a branched chain. This obscures natural relationships even in the simplest cases. One of the main reasons why phylogenetic diagrams have never been successful in certain groups of flowering plants is because the underlying relationships are too complex. A result of more importance to our discussion is that amphidiploidy may result in the immediate production of categories higher than a species. By its mere difference in chromosome number, if for no other reason, an amphidiploid is more or less isolated from the stocks that gave rise to it. If the parental stocks are distant enough there is no reason why a new genus or a new family or a new order might not originate in this manner. There is some evidence to suggest that they have among the higher plants. In this connection a paradoxical fact, first established by Darlington (1928), is of great importance. He showed that the more inter-sterile the parents of an amphidiploid, the more fertile and true-breeding is the resulting hybrid. All that is necessary, therefore, for the production of a successful amphidiploid is a single exceptional cross between species which are ordinarily inter-sterile. How wide are the limits which can be bridged in this way we can only guess. Karpechenko has experimentally produced an amphidiploid hybrid between the radish and the cabbage, which, had it occurred in nature, would easily be of generic rank. The most interesting evidence as to the limits of crossability is provided by the work of Mangelsdorf and Reeves (1931) with *Zea* and *Tripsacum*, genera so distantly related morphologically that their position in the same tribe of the Gramineae was open to serious question. These genera are, of course, ordinarily completely inter-sterile. Mangelsdorf and Reeves were, however, able to cross them by employing three highly ingenious devices. The two genera were planted in alternate rows and the maize plants were detasseled. This meant that natural pollination of the maize by the *Tripsacum* took

place not by the tens or by the hundreds but literally by the millions. Two other equally ingenious bits of technique resulted in vigorous hybrids, demonstrating conclusively that sterility between organisms is only a matter of degree and that it will be difficult indeed to set a theoretical limit beyond which crossing *might* not take place. There is, for instance, a good deal of evidence that the Pomoideae, a whole subfamily of the rose family, might have originated from amphidiploid crosses between two of the other subfamilies (Anderson and Sax, 1935). While this hypothesis is still far from proved it explains a number of puzzling facts, taxonomic, cytological and genetical, and is such a logical inference from the cytogenetical data that it was independently suggested by Darlington and Moffett (1930) in England, and Sax (1931) in this country. There is even some evidence (Anderson, 1934) to suggest that the flowering plants themselves, or certain families at least, might possibly have originated in some such fashion.

All such theories are entertaining and they are pertinent to a discussion of the origin of higher categories in the flowering plants. They are of purely secondary importance, however, in to-day's symposium. It is our business, I take it, to waste the minimum amount of time on these special features and to attempt to find principles which can be applied to the problem of higher categories in all groups of organisms.

At first sight this seems a hopeless task for a botanist. A mere leafing through of a few general discussions in the field of vertebrate paleontology turns up a set of awe-inspiring terms which seemingly have nothing to do with the plant world: metamerism, aristogenesis, allometry, heterogony, secondary polyisomerism and antero-posterior repetitive acceleration. However, when we turn from this scientific choctaw to the underlying facts we find the ground strangely familiar. W. K. Gregory, for instance, in discussing evolutionary sequences in paleontology (1936) finds that they are the results of two

cooperative principles—repetition and emphasis. He then goes on to discuss a series of related designs among the lower vertebrates. It would be possible to illustrate his general principles quite as well with plant material. The plant body is even more obviously than the animal body the result of repetition. Any flowering plant is little more than an unmistakable collection of repeated parts. The stem, its branches, twigs and twiglets repeat the same pattern even to the most intimate histological detail. Leaf follows leaf in monotonous succession, to be succeeded in the inflorescence by such obviously related structures as bracts and sepals. The operation of the general principle of emphasis can also be discerned.



Honey petals of various species of *Aquilegia* in full face and in profile.
 (a) *A. ecalcarata*, Maxim. (b) *A. viridiflora*, Pall. (c) *A. fragrans*, Benth.
 (d) *A. vulgaris*, L. (e) *A. pyrenaica*, DC. (f) *A. caerulea*, James.
 (g) *A. Skinneri*, Hook. (h) *A. canadensis*, L. Natural size. After Anderson and Schafer.

When we study a series of related species or genera we find just such changes in emphasis as Gregory has defined as the principle of anisomerism. The inevitable set of horses' hind legs from the text-books on evolution might

well be replaced by the honey-petals of the columbines (Anderson and Schafer, 1931).

From such evidence as this it is clear that we are dealing with the same fundamental processes in plants and in animals. It is the main function of this symposium to attempt to reach these fundamentals. It is, in other words, our business to consider what general laws can be applied to the deployment of genera into families and of families into orders, in such diverse groups as the flowering plants, the ferns, the fishes, the insects and the mammals. Before we can make such a direct comparison we must first consider in a general way the nature of growth in plants and animals.

It should be perfectly clear that the actual evidences we ordinarily consider in erecting genera and families are the end products of growth processes. When we classify plants, for example, we work mostly with herbarium specimens; the actual specimens are the results of plant growth. Similarly, in vertebrate taxonomy or vertebrate paleontology the actual data are derived from a series of bones and skins; these bones and skins are themselves the end products of growth. It is immediately apparent, I think, that the growth pattern, the way in which the final stage is reached, varies from group to group. The development of a mature plant is, in all but a few fundamentals, a very different set of processes from the development of a mature animal. Now it should equally be apparent that not only will a different growth pattern produce a very different end product, but it will effect, differentially, changes in that end-product. In other words, the morphological relations of genus to genus and family to family will be different in the higher plants from what they are in the higher animals by reason of the very different growth processes which lead from the zygote on the one hand to mature animals and on the other to mature plants. This connection between developmental growth patterns and phylogenetic growth patterns has been a stumbling block for some of the most acute minds in biology. A simple,

but rather precise, analogy may make it easier to discuss the matter.

Let us suppose that instead of plants and animals we are classifying two other sets of end products, rugs and pottery. Let them, furthermore, be a phylogenetic series; shall we say, for example, the rugs and pottery produced by a southwestern tribe of Indians over a thousand-year period. If our collection is complete we shall be able to divide both the rug series and the pottery series into groups analogous to genera and species. Now the point of the analogy is this, that the relation between groups of rugs as compared to the relation between pottery groups will be affected by the ways in which they are made. The process of rug manufacture will affect not only the forms of the rug, it will affect the way in which one kind of rug differs from another kind. The impingement of white civilization upon the southwest, for instance, will affect different changes in the rugs than in the pottery by reason of the differences in their processes of manufacture. Just so is it in the products of animal and plant manufacture. Higher categories have different growth patterns. As a result of these different growth patterns they also have distinctive evolutionary patterns.

A moment's comparison of plant and animal development will show how very different two growth patterns can be. The animal egg develops as a unit, the entire egg more or less simultaneously passing through a series of differentiations. The plant egg develops almost immediately into a growing point, which remains undifferentiated throughout the life of the plant, leaving behind it as it grows a continuously developing series of stages in differentiation. The most ancient oak carries at the tip of every branch a tiny fountain of immortal youth; we find maturity in the twigs, and in the main trunk we meet old age and death. The contrast between the two methods of development is so striking that few people have considered the matter. I have often wished that our leaders in the study of the blastula-gastrula-neural-groove phe-

nomena, men like Spemann and Harrison, would bring their penetrating minds to bear upon the extraordinarily different set of phenomena by which growth and development are achieved in the plant kingdom.

Lacking such an expert interpretation, I can only in an amateurish way point out some of the more obvious contrasts. Segmentation in the animal is a definite (to a botanist a most fearfully definite) process. In the plant it continues throughout the life of the individual and is by contrast very haphazard. Development in the vertebrate egg takes place, for the most part, in a precisely controlled internal environment. In the plant, on the contrary, development is immediately sensitive to environmental changes. Plant form is consequently much less definite than animal form. Trees with a particular number of limbs or leaves with a rigidly definite number of veins and cross-veins are unheard-of phenomena. In the plant world we have no such situation as that so commonly met with among the insects of a particular hair at a particular place; a single hair so definite that taxonomists can give it a name and recognize its occurrence in species after species.

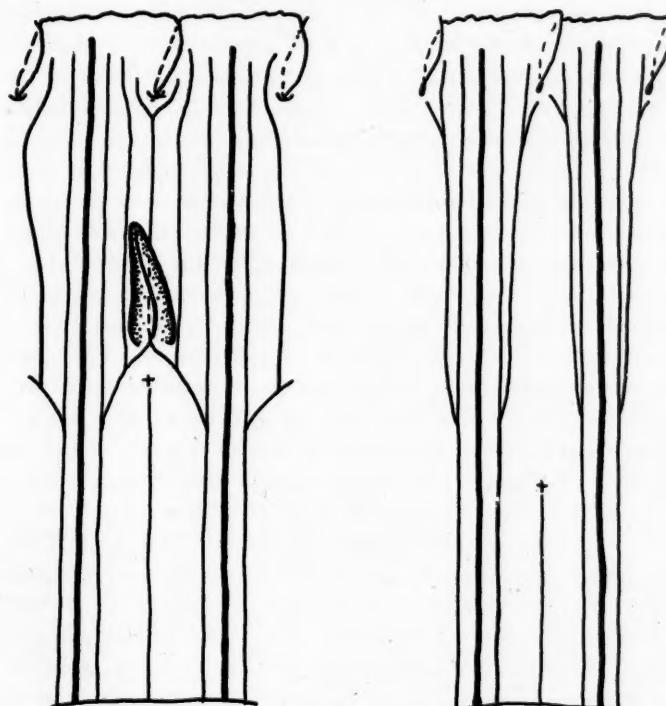
If we now return to the general evolutionary principles adumbrated by the vertebrate paleontologists and re-examine them in the light of plant and animal development we can at last get down to brass tacks. Isomerism, the repetition of similar parts, is quite as common a phenomenon among plants as among vertebrates. It is even more evident there. But as a principle determining the origin and deployment of the higher categories it does not seem particularly important. So far as plants are concerned it is mainly a phenomenon of ontogenetic interest rather than of phylogenetic import. And a botanist would suggest that its seeming importance among the vertebrates is largely due to the definite, internally controlled segmentation of the vertebrate embryo.

The principle of anisomerism, or change of emphasis, is on the other hand quite as important phylogenetically

in the plant world as in the animal. If we return to the genus *Aquilegia* we find that the series of honey petals are all built on the same fundamental pattern but differ among themselves by differences in emphasis. In the genus *Narcissus* we find that all the species possess a calyx tube and six perianth segments, with a fused crown growing out from their bases. Every species in the genus exhibits these features; the various species differ from one another merely in the way the features are emphasized. Anisomerism is certainly a general phenomenon among closely related species of flowering plants.

When we look a little further afield, however, we see a new sort of difference coming in. When we study more widely separated categories, groups of species or subgenera or genera, we find that in addition to differences in emphasis, there is a more fundamental change; there are actual differences in the pattern itself. If we turn from *Narcissus* to the related genus *Cooperia*, we find that it has in general a similar pattern but that it lacks altogether the corona or crown. If we return to the columbines, and examine their closest relatives we find that they may lack the honey gland altogether. If we review the flowering plants, group by group, we find that it is mainly just such differences as these which separate the next higher categories above the species. There will be such differences as the presence or absence of appendages in the throat of the corolla, petals that are undifferentiated in one group and differentiated into a blade and a claw in another. In the flowering plants I think we can in this way distinguish quite effectively between mere changes in emphasis and actual differentiation. Furthermore, we can state categorically that changes in emphasis are of specific rank, while differentiation separates categories higher than the species.

Here, as I see it, lies the whole crux of the problem. It is these differentiations on which the higher categories depend. How do they originate? What do they mean from an evolutionary standpoint, what from the stand-



The chief morphological difference between two groups of species of the genus *Prestonia*. In each case the diagrams show the venation of two segments of the corolla. Left, *Prestonia portobellensis*; right, *P. Riedelii*. Crosses mark the positions at which the stamens depart from the corolla tubes. The tongue-like appendage, which is the chief morphological difference between these two groups of species, is found in no related genera. From data kindly supplied by Dr. R. E. Woodson, Jr.

point of pure classification? These questions must largely remain unanswered; we have as yet so little information about the actual developmental processes in plants. Yet plant development is so comparatively simple that I think we can form a working hypothesis from mere inspection of several cases of differentiation. The relation between an organ and the forces which produced it is so transparent in a flowering plant that by such an inspection it is possible to suggest how the dif-

ferentiation took place. Let us take a simple example. In the iris family one of the pattern differences which separates genera is the differentiation of the sepal. In some genera it is a simple structure. In others it differentiates fairly early into two regions, a haft and a blade. There seems to be a force at work, part way up the sepal, a localized determiner which influences the direction in which cells will divide. Most of the cases of differentiation yield to as simple an explanation as this. The higher categories on this hypothesis originate and deploy by reason of new differentiating determiners.

What are these determiners which come into existence in various parts of the plant body and influence the origin and elongation of cells in their neighborhood? Are they such "organizers" as have been postulated in the animal embryo? They look very much as if they were. If only the science of development had been prosecuted on as broad a basis as has genetics we might be in a position to answer questions instead of asking them. In genetics we are accustomed to dealing simultaneously with both plant and animal phenomena. One American geneticist, for instance, in his actual research work jumps back and forth from *Delphinium* to *Drosophila*, from larkspurs to garbage-pail-flies, with excellent results (Demerec, 1930, 1931). The experimental science of animal embryology has a distinguished history. The experimental analysis of plant form is at long last actually under way (Avery, 1935; Sinnott, 1935). Now would seem to be the time for the lion to lie down with the summer squash and for a comprehensive study of plant and animal development to be made on the broadest foundations.

Had we such data we would be in a position to consider these differentiations which separate genus from genus and which, compounded, lead to still higher categories. How do they arise? Are they due to gene differences? We know that they effect the operation of genes; we know that in part they are under genic control (Anderson and de Winton, 1935; Sinnott, 1935). Are they themselves the

product of gene mutation? Most geneticists would immediately answer "yes," but the quick reply would be an evidence of faith rather than of facts. For my own part, I am not certain. Yet I am confident that these are questions which can be answered by the scientific method; answered definitely and in the near future. As Spemann said in his Tercentenary Lecture, "I leave you with these questions rather than with answers. For a student this is disappointing; for a scholar it is the finest thing which can happen."

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SUPRA-SPECIFIC VARIATION IN NATURE AND IN CLASSIFICATION¹

FROM THE VIEW-POINT OF PALEONTOLOGY

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THE nature of paleontological evidence bearing on supra-specific variation and the general method of this approach to that complex problem can most easily be exemplified by selecting one group of extinct animals and mentioning a few aspects of variation in that group. Following a suggestion by Professor Gregory, I shall outline some observations and opinions involved in an intensive study of the extinct mammalian order Notoungulata. The paleontological view-point on the zoological problem of higher categories, the tendencies, opinions and contributions of paleontology in this field may then be more broadly discussed. This is conveniently done within the outline laid down by Kinsey in a recent work.² Kinsey's review of this subject is the most recent and in many respects the most complete, and it is based on a remarkably thorough and profound study of an exceptionally large mass of data.

The Notoungulata were a peculiar and varied group of herbivorous mammals, most of them hoofed, almost entirely confined to South America. They were abundant there throughout the Tertiary Period, but became rare and finally extinct during the Pleistocene. Their remains were first discovered by Darwin during the voyage of the *Beagle*, over a century ago, and the first descriptions were by Sir Richard Owen. By 1890, along with the usual crop of synonyms and names based on practically unrecog-

¹ Read at a symposium of the American Society of Naturalists in joint session with the American Society of Zoologists, the Botanical Society of America, the Genetics Society of America, the American Phytopathological Society and the Ecological Society of America. The American Association for the Advancement of Science, Atlantic City, N. J., December 30, 1936.

² Alfred C. Kinsey, *Indiana Univ. Pub., Science Ser.*, No. 4, pp. 1-334, 1936.

able fragments, about ten really valid and well-characterized genera were known, all of later Tertiary or Pleistocene age.

The first genus recognized, in a sense the type of the whole Order, was *Toxodon* Owen, 1837, from the Pleistocene. It was a large animal, about the size of a small rhinoceros and of similar stocky build. Its incisors were specialized into an apparatus suitable for cropping vegetation, and its grinding teeth had very high, strongly curved crowns, whence the name ("bow-tooth"). Another classic genus *Nesodon* Owen, 1847, is manifestly related to *Toxodon* but is older, Miocene, and is smaller, more slender and in general more primitive. Both genera belong to one of the usually recognized primary divisions of the Notoungulata, the Suborder Toxodonta.

Another group of classic genera, including *Typhotherium* Bravard, 1857, *Interatherium* Moreno, 1882, and *Hegetotherium* Ameghino, 1887, is based on smaller animals with gnawing anterior teeth and high, prismatic grinding teeth. These false-rodents are related to the rhinoceros-like *Toxodon*, but because of their rodent-like aspect and a few more detailed characters they have been united in another suborder, Typhotheria.

Homalodotherium Flower, 1873, from the Miocene, is a large animal comparable to *Toxodon* in size but with extraordinarily different proportions, its clumsy legs elongated in a peculiar way and its toes ending in large claws, rather than hoofs. Its teeth are low-crowned, in continuous series and relatively unspecialized. *Homalodotherium* is certainly a notoungulate, but it is so unlike the toxodonts or typhotheres that it is generally placed in a third suborder, Entelonychia.

In the Toxodonta and Typhotheria the limb structure is almost the same throughout, with rather unimportant modifications mostly correlated with bulk and speed. Their type of limb structure is primitive for the Notoungulata as a whole and in them never underwent any profound modification. Their teeth, on the other hand,

became highly specialized, and in this respect the later genera are almost unrecognizably different from the earlier. This radical change occurred rapidly, between the early Eocene and some time in the Oligocene, then becoming stabilized and not undergoing any very important further changes before the extinction of each group, some of them in the Pleistocene.

In the Entelonychia the teeth never became so highly

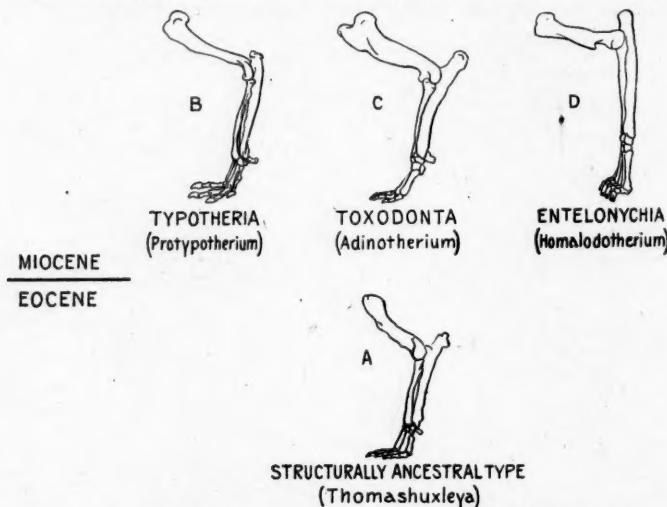


FIG. 1. Fore-limb evolution in some notoungulates. *Thomashuxleya* approximately represents the primitive structure ancestral for all. In typical toxodonts and typotheres this is not much modified. In the entelonychians, however, it is greatly changed in form and in function. The Miocene forms shown are all contemporary. Lateral views of left forelimbs, brought to equal size for comparison. A after Simpson, B after Sinclair, C and D after Scott.

specialized. There were changes, of course, but in essentials the latest entelonychians, in the Miocene, had dentitions of early Eocene type. The limb structure, however, was deeply modified, and there is reason to believe that the major changes in this respect were rapid and concentrated in one part of the history of the group. Successive genera that are almost identical in the dentition are pro-

foundly different in the limbs, just as some successive genera of typotheres are hardly distinguishable in the limbs but very distinct in the dentition.

These examples illustrate phenomena of wide importance in the study of supraspecific variation. Within a single group, such as the typotheres, one set of structures, such as the limbs, may be relatively invariable, evolving

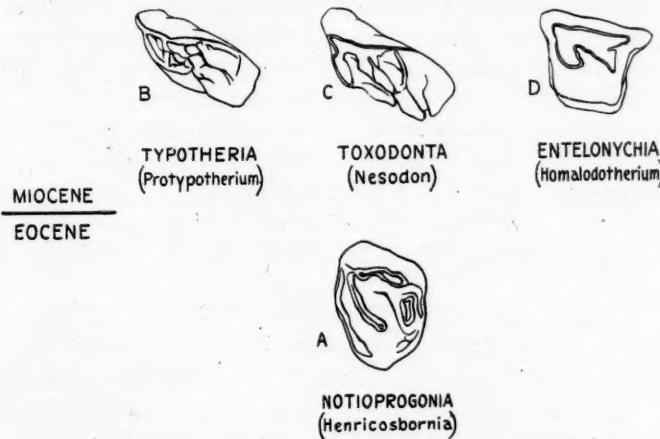


FIG. 2. Upper molar evolution in some notoungulates. *Henricosbornia* approximately represents the primitive structure ancestral for all. In later toxodonts and typotheres this is profoundly modified (also strikingly in the height of the crown, not obvious in this view). In entelonychians there is relatively little change (the height of the crown also remaining relatively low). Crown views of left last upper molars, brought to equal size for comparison. A from specimen, B and C after Sinclair, D after Patterson.

slowly and remaining primitive, while another set, such as the teeth, in the same group may be highly varied and variable, evolving rapidly and becoming specialized. Two different supraspecific groups, such as the toxodonts and the homalodotheres, may be essentially distinguished not so much by the general conservatism of one or by its uniform divergence, as by the fact that different parts of the organism remain primitive and different parts are specialized in the two groups. Moreover, degree of variability and concomitant rate of change in a progressive set of

structures, as in the typothere dentition, is not necessarily constant but frequently characterizes a limited period and is preceded and followed by long periods of relatively low variability and little change.

Students of phylogeny often tacitly or explicitly assume that a constant rate of evolution within one group or within related groups has been the rule, but if so it is a rule with so many exceptions that it is not a safe guide. Differences in rate of evolution between different structures in the same phylum, between different periods in the history of one phylum, and between different phyla with a common origin have certainly been very common. These different rates of structural modification, which are generally accompanied and are probably in large part caused by different degrees of variability,³ are among the most important factors in the differentiation of supra-specific groups.

From the nature of these differences in rate, it follows that groups comparable in taxonomic scope or in structural distinction or variety did not necessarily arise at comparable times. One family of mammals, Didelphidae, arose in the Cretaceous and another, Ursidae, in the Miocene, an enormous difference, and yet by other and more useful criteria than time of origin these are both properly ranked as families in the taxonomic hierarchy. Such facts invalidate some inferences or prejudices regarding mammalian history, such as the argument that the family Hominidae must necessarily be comparable in antiquity with the other families of primates or that it must have developed at a comparable rate or at one equally constant.

These considerations lead farther to the taxonomic problem as to whether different groups of the same formal

³ Throughout this paper variability and variation are used to designate physical differences in related animals without attempting to distinguish differences resulting from various causes, distinctions extremely difficult or impossible to make from paleontological materials. It is probable that most of the differences involved in the examples given were heritable and had a genetic basis.

rank, for instance families, are or can be made equivalent by some criterion such as time of origin. It would take too long a digression to discuss this problem here, but it may be affirmed that this time criterion, at least, is impractical and quickly leads to confusion and to absurdity. Absolute equivalence between families (or other units) of different zoological divisions, such as fishes and mammals or, *a fortiori*, insects and mammals, does not exist and is probably quite unattainable, but a reasonably satisfactory working compromise can be reached.

Returning to the Notoungulata, the three-fold division into Toxodonta, Typotheria and Entelonychia, which has been outlined above, arose about 1895 and in various forms this general, simple arrangement has been widely used ever since. It is an admirable system as far as the well-differentiated and relatively impoverished faunas of the Miocene to Pleistocene alone are considered. Even in the Miocene the characters of the various phyletic lines within these groups were definitely fixed and the problem of the origins and of the basic relationships of groups hardly exists as long as attention is confined to these reliques.

As early as 1897, however, the great Argentine paleontologist Ameghino began the description of much earlier faunas, some from well down in the Eocene. Many of these earlier South American notoungulates do not fit into the three usual suborders, and they give a very different picture of the development of the Notoungulata from that based on the later forms. Ameghino's solutions of the problems presented have not been accepted in their entirety by other workers. It would be unfair to attempt a résumé of his views here, for they were complex and full justice would demand a somewhat detailed analysis of the many largely unappreciated but really valuable and enduring parts of his work, and the distinction of these from the more superficial but more obvious points on which he is now generally conceded to have erred. The point most pertinent here is that in almost every group of notoungulates Ameghino observed two sorts of morphological re-

semblances: one to other South American groups of earlier or later age and the other to various Holarctic groups. The observation was, in general, both accurate and acute and all the resemblances mentioned exist and are important. In interpreting these results he concluded that both resemblances were evidence of actual phyletic relationships, so that the various Holarctic ungulates were considered as derived from analogous notoungulates. This theory, or rather complex of theories, has had to be abandoned, for it has since been demonstrated that the resemblances to Holarctic groups are almost entirely superficial and adaptive and not due to any close relationship.

An instructive example is provided by the Notohippidae, a family of Notoungulata which, as the name implies ("southern horses"), was supposed by Ameghino to be related to, and to be the source of, the Equidae of our hemisphere. The resemblance is largely confined to the dentition and is most noticeable in the development by both groups of high-crowned, prismatic cheek teeth, enveloped in a heavy layer of cement, and with a complexly folded pattern of enamel crests which is mechanically or functionally very similar in the two groups. Now that the history of these teeth is very well known for the Equidae and can be inferred with a high degree of probability for the Notohippidae, it is shown beyond any question that the development is independent but closely parallel in the two groups.

Both start with low-crowned, cementless, sublophodont teeth in the early Eocene. These initial stages, like the final development, are functionally closely analogous. There are, however, differences in the exact relationships and structures of the individual elements, cusps, crests and valleys, of the teeth in the two families, and these distinctions are maintained throughout their history. On this heritage, which is relatively invariable within each group, there are imposed new, progressive characters, mainly hypsodonty, lophodonty and a cement investiture,

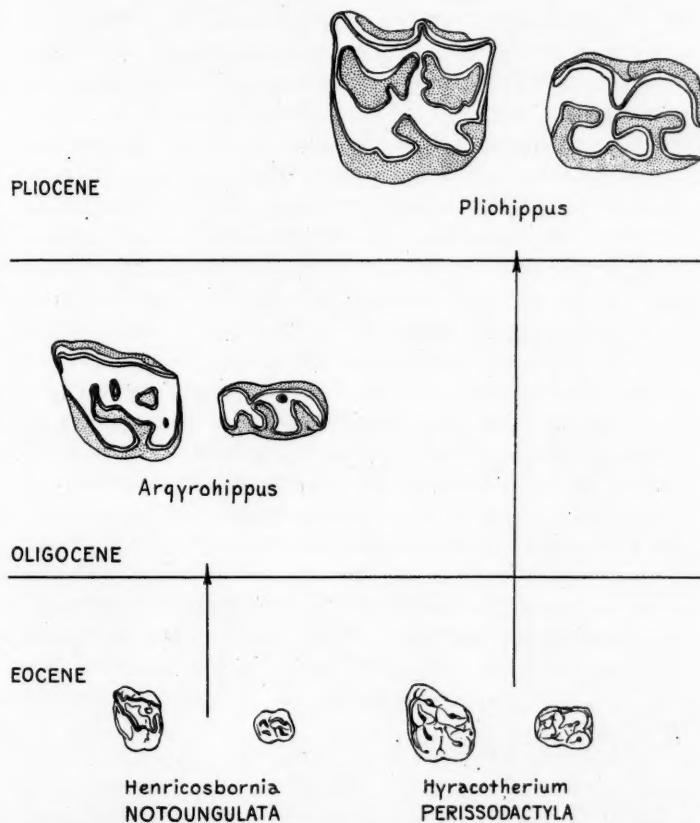


FIG. 3. Analogous evolution in distantly related groups of mammals. The notohippids among notoungulates and the horses among perissodactyls both developed high-crowned, fully lophodont, heavily cement-covered molars, closely similar evolutionary tendencies appearing independently in the two groups. Even in the Eocene, however, the relatively simple and primitive teeth structurally ancestral to the two had basic structural distinctions in the connections and development of the various cusps and crests. These constitute the heritage of each group, and subsequent development does not obliterate this heritage, so that the patterns remain quite distinct. Each has its own family and ordinal characters which evolve and vary, but which are recognizable from first to last. The notohippids reach a stage of structural advance, or a *habitus*, in the Oligocene which the horses did not achieve until the Pliocene, although they were structurally on about the same plane at the beginning of the Eocene. Crown views of second left upper and second right lower molars. All natural size. From the specimens.

and these are the same in both groups. It seems that there is a basic and relatively constant structure within each line to which are added new factors, or an accretion of mutations, that are the same for both but that appear in them independently. This independence is further emphasized by the time and rate of appearance of these mutations. The true horses continued with relatively little change in these respects through the Oligocene, underwent a pronounced acceleration in the Miocene, and reached essentially the terminal condition at about the beginning of the Pliocene. The notohippids underwent a rapid development, perhaps at about the Miocene rate of the Equidae but at a much earlier time, in the Eocene. In the Oligocene they had already reached a condition about equal, in these respects, to that of the horses in the Pliocene. The notohippids then became extinct, despite the development of what would seem to have been the most efficient herbivorous dentition in the world at that time. Without straying too far into the tempting bypaths of speculation, may it not be that this remarkably early and rapid dental development was not matched by the correlative progress of other necessary factors and that the organism as a whole was thrown into a fatally unbalanced condition?

Aside from a rejection of Ameghino's views, which in many cases was unfairly sweeping, little constructive work on the early notoungulates was done by any one else until recently. Now the whole subject is reopened on a new and much more satisfactory basis. Ameghino's priceless and classic specimens, which were never definitively published and which a combination of circumstances long made unavailable for research, have now all been restudied in the light of later knowledge. Important new collections have been made, greatly increasing the number of specimens, permitting a good study of variation for the first time, revealing skulls and even skeletons of animals hitherto known only from isolated fragments and unearthing a number of new species and

larger groups and at least one fauna older than any described by Ameghino. These and other factors have produced a revolution of ideas concerning this great mammalian order. In the state of flux into which the subject is thus plunged at present, conceptions of supra-specific variation and principles of phylogeny and taxonomy, which tend to be taken for granted during the more gradual evolution of knowledge, are brought into prominence and subjected to a severe test on a grand scale.

One of the first conclusions to emerge from this recent research was that many early notoungulates, indeed the majority in the oldest Tertiary formations, do not enter in a natural way into any of the three classic divisions of the Notoungulata: Toxodonta, Typotheria, Entelonychia. There had been some tendency to refer these to the Entelonychia, because they had been known almost entirely from the teeth, which resembled those of later entelonychians more than they did those of later toxodonts and typotheres. Now it plainly appears that the earlier toxodonts and typotheres also had teeth of this same general type, or in other words that supposed entelonychian characters in the dentition were merely primitive characters of all notoungulates, which happened to be less modified in entelonychians than in most other groups, as has already been suggested.

It appears rather that there was toward the beginning of the Tertiary a somewhat unified but extremely varied group, a sort of reservoir of phylogenetic potentialities, from which the classic groups derive. Within this ancient notoungulate complex there were numerous different minor phyletic lines, each of which was tending to be modified in its own direction and at its own rate. The classic groups merely represent such few of these lines as were successful in surviving into the Middle and Late Tertiary. Concordant with their longer history, these groups eventually came to differ more markedly from each other and from the common ancestry than did the much more numerous lines within the Early Tertiary com-

plex. As a convenient means of designating these manifold, relatively primitive earlier forms I have proposed that they be classified as constituting a suborder of notoungulates under the name Notioprogonia. The notioprogonians include the structural ancestry or basic stock of notoungulates generally, and they also include a number of divergent phyla which died out before either their structural distinctions or their morphological variety were sufficiently great to warrant their being set aside in special suborders in a practical scheme of taxonomy.

An outstanding characteristic of the Notioprogonia is extraordinary variability, manifested in two ways difficult to distinguish but apparently really different: individual or infra-specific and phyletic or supra-specific.

In some cases it has now been possible to bring together large collections all of one geologic age and from one locality. With such material it is possible to recognize and delimit natural minimum group units, conventionally recognized as species, with considerable assurance and exactness. It is impossible here to go into details as to the criteria and methods employed, especially as they are rather laborious and many of them are new to paleontology, but I believe that biologists generally will recognize their validity. The general purpose and result was to recognize a sample of a population in which many variations appear, as in all populations, but in which these variations were arising in a single interbreeding community and with little segregation in definite components of the population.

An example is afforded by a sample of last upper molars of *Henricosbornia lophodonta* Ameghino, a notioprogonian common in the Eocene Casamayor Formation. A good, unified sample of 33 specimens shows a range in width of 5.8 to 7.1 mm, a difference of about 20 per cent., with an approximately normal distribution around a mean of $6.41 \pm .06$. Other dimensions vary to the same degree, and the variation in structure or in non-numerical characters is also well marked, as is suggested by the

accompanying figure of selected teeth showing the most abundant (or modal) structural type and also the relatively rare extremes of deviation from this. Different as these are, they all intergrade, and it is also noteworthy that to some extent the differences can be analyzed into single factors, such as round or long metaconule, attached or detached metaloph, strong or weak crochet, etc. In general, these show no significant association with each other, that is, groupings made on one of these characters do not tend to include the same individuals as those based on others. This is one of the lines of evidence that the sample is unified and does not consist of two or more dis-

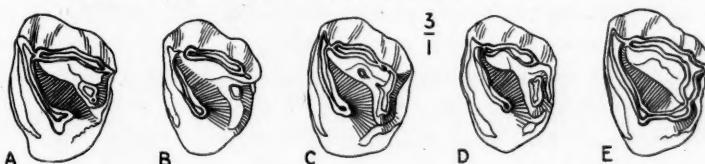


FIG. 4. Structural variation in M^2 of *Henricosbornia lophodonta*. Although these teeth all belong to a single species and are from exactly the same horizon and locality, their differences in quality and in quantity are as great as commonly occur between related species or even supra-specific categories. Segregation of the variants into separate lines of descent would lay the basis for the rise of higher categories. All three times natural size. From the specimens.

tinct segregated zoological phyla. Differences in the other parts of the dentition are analogous in kind and in degree to those shown.

A single student, Ameghino, with all the material then known before him,⁴ based three families, seven genera and seventeen species on specimens all of which now seem almost certainly to belong to this single species, *Henricosbornia lophodonta*. The case is extreme, perhaps unparalleled in taxonomic history, but such multiplication of synonyms, on a smaller scale, occurs in the work of every active paleontologist and is in some degree unavoidable in this science. The statement is no indictment of

⁴ Which was abundant but did not include the sample here discussed or any comparable sample from which a good criterion of individual variation could have been derived.

Ameghino's ability, which was exceptionally great, but it introduces two important considerations: The need for and difficulty of obtaining an idea of the extent of variation within any one paleontological species, a topic outside the scope of the present paper, and the fact that the difference between infra- and supra-specific variation is often, or essentially, distributional rather than either qualitative or quantitative.

As regards this second point, Ameghino was using criteria which were valid in the groups from which they were derived and the application of which in this case, where they are not valid, followed what is still considered sound practice and was opposed by no apparent *a priori* consideration. The fact is that the differences between several of these variants of *Henricosbornia lophodonta* are exactly analogous both in kind and in degree to differences which do sometimes distinguish groups of generic and even of family rank, that is, they may be distinctive and relatively constant characters of different phyla and groups of phyla, each including several species, although here all are mingled in one species. For instance, so simple a character as the degree of attachment of the metaloph to the ectoloph is relatively constant in the Equidae, and differences in this respect in that family may define successive genera or may differentiate contemporaneous phyla, yet in *Henricosbornia lophodonta* every condition from almost complete independence (Fig. 4B) to almost complete union (Fig. 4C) occurs. Moreover, in notoungulates differences analogous to these may also characterize quite distinct supergeneric groups. For instance, in the Notohippidae two groups of genera, one typified by *Rhynchippus* and one by *Notohippus* itself, are differentiated by a relatively constant difference in the height on the crown at which two minor enamel folds, first and second cristae, merge.⁵

⁵ Of course this is not the only difference between the two groups, but it is representative of a number of differences each more or less analogous to this.

The difference between the morphological characters of a small unit, called a species for present purposes, and of a group category, genus, family, order, including several of these units, may thus be quite different from the usual picture (which is, however, also valid in other cases) of the larger group being constituted simply by accretion of successive individual variations or mutations. In the basic unit, each character varies within the whole group as such. Every character has, so to speak, a certain repertory of variability which involves all the individuals of the group. This is true of the variations shown in *Henricosbornia lophodonta*, and these differences are infra-specific in this case. The higher categories are defined by characters which still vary, inevitably, but the variation of which is not confined to such narrow limits, is not from one individual to the next but is relatively constant within each small unit and shows its range of variability from one species to another.

From this point of view, *Henricosbornia lophodonta* is a potential ancestor of several different genera which would at first differ from each other little more than do the individuals of this species. If one or a few of these variations were segregated into one line of descent, so that variations of this particular sort always occurred, or more frequently occurred, in that particular line, a supra-specific evolutionary phylum diverging from the parent group in a fixed direction would arise. Continued elevation of variations from the individual to the group category would lead to continued divergence.

Another phenomenon which seems often to be involved in such a history is that two variations that have been apparently independent, for instance, the development of a crochet and the attachment of the metaloph, may become linked so that a strong crochet is usually or always accompanied by an attached metaloph. In such a case the characters may vary independently on an infra-specific level, but be positively correlated on a supra-specific level, yet the difference between the two types of variation lies only

in the correlation, not in any qualitative or quantitative difference in each character.

The reasons for these phenomena are doubtless genetic, and they clearly could be described in genetic terms. This need only be mentioned here, since the present task is to present strictly paleontological observations, but it is important to indicate that there is no natural barrier between genetic and paleontological research and that both must eventually unite in any final synthesis of modes of evolution.

In spite of the difficulties that we are now finding in tracing out the early phyla within the Notioprogonia and from that complex into the later notoungulate suborders, the general potency of such a group and the mode of its differentiation into various supra-specific categories is shown by such examples as that here briefly sketched.

With this indication of the bearing of a particular research problem in paleontology on supra-specific variation, attention may next be directed to the broader problems of higher categories in general and the bearing of present paleontological opinion and data on these problems. As already stated, this will be fitted into the outline provided by a recent work of Kinsey (1936, cited above). He gives a list of thirteen concepts or principles that seem to him to underlie most zoological work on higher categories, and as these include almost the whole field of thought on this subject it can be well covered from the present point of view by quoting these and adding what seems to be the best or the most generally held paleontological opinion on each concept. As first phrased and here quoted, these concepts are expressed by Kinsey largely for the purpose of attacking and rejecting, or at least of markedly modifying them, and are not his own opinions. His opinion on each has, however, been considered in each case and is found to be of the greatest value to the paleontologist, even when it can not be entirely endorsed from our materials.⁶

⁶ Kinsey disarms difference of opinion by suggesting that it be based on studies as extensive and complete as his work on *Cynips*. This work is, in-

(1) "Higher categories represent the ancestral stocks from which the lower categories . . . have been derived." This principle, stated in this form, is not accepted literally by paleontologists, the difficulty being in the definition of the word "represent." We suppose, for instance, that the genus *Equus* is a higher category derived from a lesser group within the genus *Pliohippus*. The characters distinctive of *Equus* are not those that characterized its ancestral lower category in *Pliohippus*: if this were true *Equus* could not be distinguished from *Pliohippus*. Nevertheless, the particular species, or similar lesser group, ancestral to a genus may usually be recognized by its possessing characters distinctive from other contemporaneous groups which pass into the contiguous species (not necessarily into all the species) of the descendant genus.

(2) "The ancestral stocks which gave rise to the higher categories were originally single species." The old question of monophyly and polyphyly is still not settled theoretically. In practice the paleontological consensus seems to be that natural groups may and often do arise

deed, so extensive and so complete, based as it is on more than 35,000 individuals of one genus (not to mention 124,512 galls from which physiological differences could be deduced), that it is a truly monumental and in many respects incomparably fine work. The mammalogist can never gather comparable collections, indeed it is probable that there are whole mammalian genera of which 35,000 individuals do not exist even outside of collections. The paleontologist is still more limited. Most paleontological work is based on single specimens. To the extent that this is unnecessary, no apology is possible, and on the contrary I and other paleontologists have repeatedly urged that our science must begin to emphasize groups and abandon its devotion to the individual. Yet at best 50 or 100 individuals of one species, and each only represented by a fragment of the whole individual, is all that can be asked for in a paleontological sample. Yet this numerical inferiority surely does not deny us a voice, or even at times a decisive vote, in evolutionary studies. There are, too, problems on which infinite material and attention as regards a limited group, and the genus *Cynips* is, after all, a very small category, can not be decisive, and this question of higher categories is just such a problem. It demands not only such intensive studies, with their own irreplaceable and invaluable results, but also, and perhaps even more, the study of truly high categories over long evolutionary periods, data that can only be supplied by paleontology.

polyphyletically in the strictest sense, and yet that they are natural. For instance, it seems probable that *Merychippus* arose by independent but parallel mutations from a group of two or more species of *Parahippus*. But these species of *Parahippus* were themselves very closely related and were beyond much doubt ultimately derived from a single species. Hence in theory we do believe that a genus is derived from a single species even in such a case, but as a practical morphological taxonomic problem we sometimes necessarily draw the taxonomic categories in such a way as to place the earliest species of what is to become a descendant genus within a special group (such as a subgenus) of the ancestral genus. A

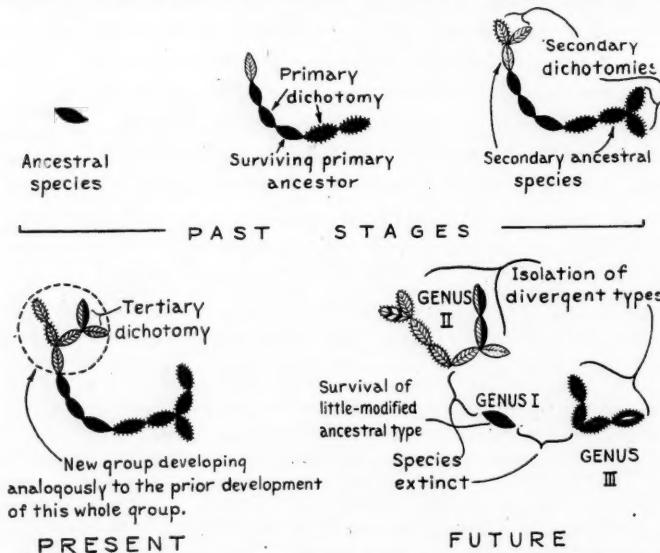


FIG. 5. Diagram of the chain-like and also branching development of species in time. The condition here designated as "present" is essentially like the patterns of species found by Kinsey in the genus *Cynips*. It implies a step-by-step, branching development in the past, essentially like that shown. Paleontological examples show that it also implies a future disappearance of some of the links, resulting in a separation of the branches and a pattern more or less like that given as "future." The single species shown as the first past stage is itself a terminal link in an older, similar series of species.

better generalization, one that is basic in paleontological taxonomy and that I believe to be demonstrably true, is that a higher category is always derived from a single lower category, the lower category not necessarily being as limited as a species or as the minimum natural unit.

(3) "The higher category is of more ancient standing (in time) than any lower category." This assumption is perhaps made by neozoologists, but to the paleontologist, who is most intensely concerned with time, it requires modification or definition if it is to have any meaning. A genus does not give rise to its included species. Since a genus is a group of species, if it exists at all it must, by definition, simultaneously include one or more species. A higher category, as such, thus can not be older than all the lower categories within it in this sense. In another sense, however, the generalization is certainly true. The dichotomy that produces a branch destined eventually to assume the rank of, say, a genus in taxonomy is necessarily older than the dichotomies that produce a second, third, etc., species along that branch (or chain). But it is essential to bear in mind that the ancestors of the genus also belong to species, and that eventually the group is traced back not to a higher category arising as such but simply to a species of an older genus.

(4) "The ancestral stocks (ancestral species) representing the higher categories are for the most part extinct." That the single smaller category, often or usually a species, from which our various higher categories arose is usually now extinct is certainly true, and it becomes more probable the higher the category involved. Kinsey is dealing with a group in which the connecting links (in the true sense of those abused words) seem not to be extinct, yet his exception does not controvert the rule. Furthermore, he is dealing with supra-specific categories, to be sure, but nevertheless with low categories, below the genus. The links between classes, orders, families and genera are almost all extinct, and so are many of those between species, at least among vertebrates, whatever

may be true of insects. No chain now living links mammals and reptiles, perissodactyls and artiodactyls, camels and antelopes, South American and Old World camels or dromedaries and Bactrian camels, and this is not due to lack of discovery of living forms. The links between all these groups, from species to class, are fairly well known paleontologically and are all extinct. The time of extinction of the links (which I would rather liken to the crotches

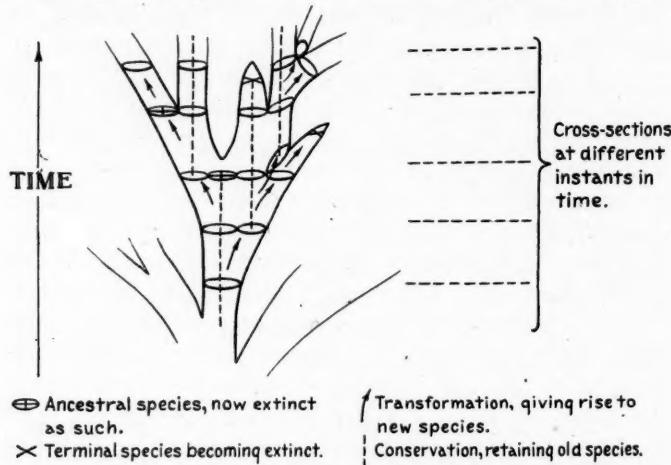


FIG. 6. Diagram of part of the tree of life or pattern of branching phyla as developed in time, showing the relationship between such a pattern and that of chain-like series of species appearing at any one time, and the existence within the pattern of persistent ancestral species, of extinction and of transformation.

between branches) is older the larger the categories: in the example given the times are approximately Triassic, Paleocene, Eocene, Miocene and Pliocene or Pleistocene, respectively. Here again is seen the sense in which it is true that the higher categories are older than their included lesser categories. It has already been emphasized that this does not mean that categories of the same rank are of equal age.

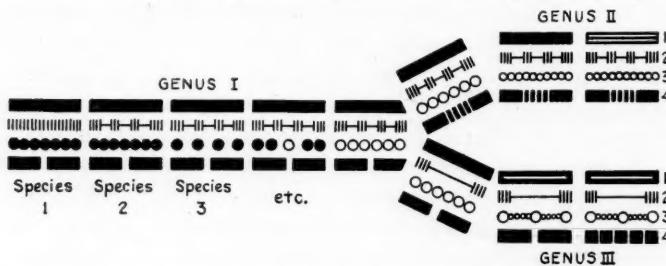
(5) "The characters common to all the elements of a higher category represent characters which were found in

the ancestral stock (the species) from which the category was derived." On this Kinsey remarks that it would be logical if all the elements of a higher category did have characters in common, but that it is often found and might be invariably found if all the facts were known "that no single character applies to all the species of a genus." This statement can not be taken literally, for it is obviously untrue. All species of *Cynips* have wings (whatever their size), all have tracheae, all have six legs, all make galls, and so on for many characters, probably many hundreds, that they all have in common. The objection becomes valid, however, and also important if it is expressed that a higher category does not necessarily have any set of characters common to all its included units and not occurring in any separate, related category. Paleontologists are finding this to be more and more the case, especially in dealing with such dynamic things as phylogenetic categories in time. For instance, I do not know any one character that occurs in all toxodonts and in no typotheres. When this is true, which is not always but becomes increasingly common with increasing knowledge, taxonomic definition is made difficult but not impossible. We introduce a fourth dimension, time, and define the higher category not by a fixed set of characters at any given point in time but by the transmutation of its characters throughout its history, a fluid character embracing the group as a whole and always distinctive from any similar related group.

(6) "The higher categories are realities in nature. They were once real species." This is the most important point involved in the present discussion. Kinsey strongly opposed this principle and most of its implications. Most paleontologists will agree with Banks in believing that the limits of taxonomic categories are often undefinable in practice, since in the nature of evolution one grades into the other, but that both species and higher categories are real.

To demonstrate the conviction that supra-specific groups do have an objective reality, I have taken the lib-

erty of copying a figure given by Kinsey to prove the opposite contention, leaving the objective data as he gives them but changing the taxonomic interpretation. The dichotomous development with which the paleontologist



DEFINITIONS OF GENERA			
	Genus I	Genus II	Genus III
Character 1	Constant: 	 to 	 to 
Character 2	 to  to  to  to 	 to  to  to 	 to 
Character 3	Highly variable	 to  to  to 	 to  to  to 
Character 4	Constant: 	Constant:  to 	 to 

Characters and **000000** occur in both Genera **II** & **III**, are also present in Genus **I** species **5**, and show that species, and no other of Genus **I**, to be their common ancestry.

FIG. 7. Relation of higher categories to the more variable characters within a chain of species. The diagram representing concrete data on characters is from Kinsey (1936, Fig. 14); the interpretation and conclusions are quite different. The subdivisions here arbitrarily labeled "genera" are higher categories and are different in kind from the species, but are equally real and natural. Their definition does not presuppose that each has a combination of characters exclusive to it and constant within it, although this happens to be true in this case and often is true in nature. More closely related species have more in common. Genera II and III derive a visible common heritage from the single species of Genus I that is ancestral to both. The interpretation is not dependent on whether all the species survive to coexist at any given moment or whether, as will in any case inevitably happen sooner or later, some of the links in the chain disappear. In addition to the few and variable characters shown, there are a vastly greater number of characters that are constant or nearly so throughout the whole group or within its subdivisions.

deals has dichotomy in time, whereas that shown by Kinsey is developed in space, but the difference is not essential. This dichotomy is an objective fact, assuming that

the data have been correctly interpreted, and is exactly the process by which new groups are supposed to have arisen from one ancestral species. The status given these groups, species, genera, families, or whatever it may be, is arbitrary but the groups themselves are natural. Kinsey's figure might be interpreted in any of several ways, taxonomically, but that here given seems to establish the point. Kinsey's own interpretation is not in accordance with the reality of higher categories, but it seems open to objection to make such an interpretation and then to argue from it that categories are unnatural, when a natural arrangement of the data can, in fact, be made.

In this instance there are generic characters that are constant within each group designated by me as a genus. Thus the combination of characters shown as 1 and 4 is diagnostic of Genus I, 2 and 4 are diagnostic of Genus II, and 2 is diagnostic of Genus III. It happens that Kinsey has shown these as constant within the given groups. If this were not true, it would be more difficult to define the genus, but the reality of the genus would not be changed, nor would definition be impossible. For instance, Genus II can be defined not only by the constant characters 2 and 4, but also by the changes in 1 and 3 which take place in this line and in no other. The figure also shows the point that in a given stage, for instance, the first species of genera II and III, the characters common to the divergent species, such characters here being 1 and 3, occur in the one species ancestral to both of them. To the best of my belief, however, no paleontologist or zoologist would really support the view, which is stated by Kinsey only for the sake of demolishing it, that these characters 1 and 3 must then appear unchanged in all the descendants of that species.

The paleontologist is familiar, more than the zoologist, with the usual absence of discontinuities in phylogeny, and he does not suppose his taxonomy to rest on a basis of discontinuity. What it does rest on in theory and in practice as far as the latter is successful is, however, a sort of discontinuity, that between branches, as may be seen in Kin-

sey's diagram. They are separate, and their union both to a single base does not mean that the separation is artificial.

In reference to this figure one more point must be made, which is that such a figure can be derived from actual data only by selecting a few characters deliberately such that they all (four in this case) differ in the end. There will

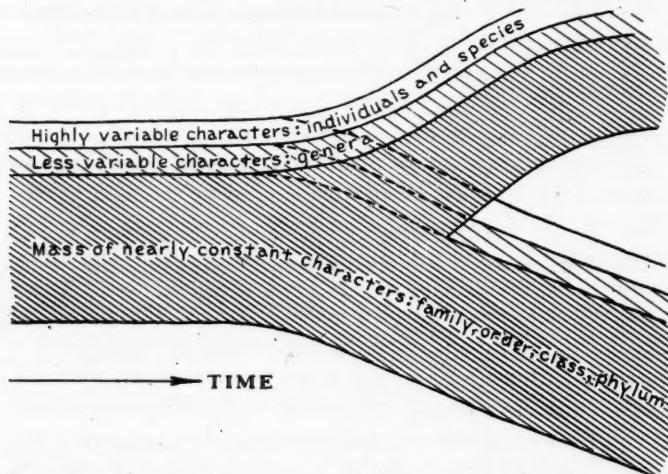


FIG. 8. Diagram of characters in a branching phylum with respect to their variability. The great majority of characters in any species within this phylum are relatively constant throughout. They are inherited from a very remote ancestry and their variation is distributed over great categories, larger than this phylum, so that within this small section they appear practically invariable. The characters that change rapidly in time and that are highly variable at any given time are always fewer in number. They are involved primarily in the evolution and in the recognition of the lesser categories. It is not meant to imply that the same characters remain in any one channel of this stream-like diagram. On the contrary, given characters are constantly passing from the "highly variable" to the "less variable" channel, etc., and this is an essential phenomenon in the origin of higher categories.

be vastly more characters in which the terminal species do not differ appreciably, characters which are, in Kinsey's example, common to all *Cynips*, those common to all wasps, those common to all insects, and so on, for of course such characters also exist and vastly outnumber those distinctive of the species. They are perhaps to be taken for

granted, but they are of the nature of the problem, for they do probably represent a general inheritance from a common ancestry and they are relatively invariable characters defining objective supra-specific categories.

(7) "Evolution has been radiate, not linear." Paleontologists believe that it has been both radiate and linear. The effect of radiation is usually achieved by a series of dichotomies. Individual phyla are linear (although not always rectilinear) and a higher category consists essentially of a number of such lines radiating, or better diverging, by successive dichotomy from an originally unified ancestry. As Kinsey's own interpretations (*e.g.*, Fig. 13) seem to me to exemplify this process very much as a paleontologist understands it, it is unnecessary to labor the point.

(8) "The picture of evolution is, therefore, that of a 'tree of life'." To a paleontologist there seem to be two flaws in the classic figure of phylogeny as a tree. The first is that linear evolution has been, in fact, very common, so that the habit of the "tree" was not that of, say, an oak, but was one with innumerable long branches, often occurring in parallel clusters. More important is the fact that the idea of an ancient trunk and terminal twigs for the present-day species overlooks the extraneous or accidental nature of "the present day," for the present is merely one of an infinity of possible cross-sections of the history of life. At any time, wherever the cross-section be taken, life consisted of species. There was no time when there existed only large branches, the classes, for instances, with no twigs or species. There was, however, a time (different for each class) when the ancestry of that class was single, but it was then a single twig, a species. In short, the tree, or better the vegetative and branching figure, comes closer to reality when it is considered as a growing plant. The adult tree represents only present conditions, not history. The seedling of the same tree represents the time when the higher category was beginning to develop. No figure that leaves out time can represent history. Such figures are in any case imperfect

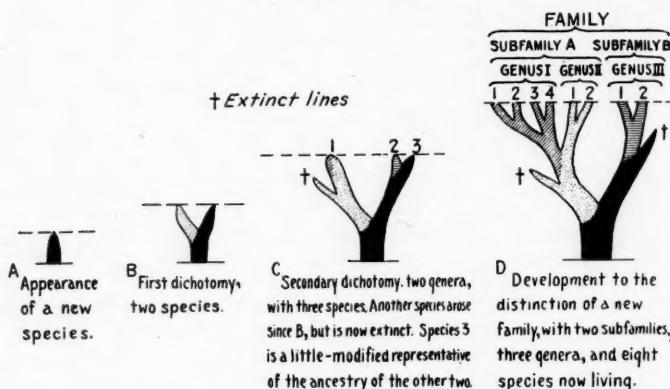


FIG. 9. Diagram of the growth of part of the Tree of Life. All that actually exists at any given moment is the terminal twigs, those that touch the broken horizontal line in each figure. The trunk in D does not and never did exist as such; when it had concrete existence it was not a trunk but a twig (A). But it still represents figuratively the twig (A) that has given rise to the whole tree (D), and it is also the diagrammatic equivalent of the bracket under the word "Family" in D. Each of the brackets similarly corresponds with some one trunk or stem on the tree, which in turn corresponds with what was at some previous time a single species, a twig. All the categories are real and are based on the branching and transformation of the growing tree, but the taxonomic arrangement at any one time, as a practical matter, will depend on the degree of transformation and the extent of branching that are known to have occurred. Thus if we have the whole picture D before us (as represented by the concrete paleontological materials), the group might be recognized as a family and probably the ancestral species seen in A would also be placed in that family, but if only A is known, the rank of family is not indicated and the species seen in A will probably be referred to an older family, along with the species that gave rise to it.

representations of facts which, after all, are not logically connected to the figure. It is easy to belabor and criticize them because they are imperfect, yet they do form valuable aids to visualization and in teaching as long as the imperfections are realized. I believe that most zoologists do realize these imperfections. Kinsey prefers the figure of a cactus, and with his data this evidently is a better aid to visualization than a literal tree, but both are branching vegetative figures and the difference does not seem important.

Kinsey further claims that the tree figure, which he strongly opposes, should mean that the species ancestral

to a higher category "disappears with and because of its subdivision into its consequent derivatives." If the figure involves this principle (which does not seem to me to be necessarily true), this is one of its imperfections that is well understood by paleontologists. We know, and zoologists in general do really seem to accept this, that an ancestral stock very often continues with relatively little modification long after it has given rise, by branching, to one or more groups of divergent or of more rapidly evolving character. An outstanding example is that of the living opossums, which are very little changed from the ancestry of all the marsupials. Although alive to-day, they are in a true sense the ancestral stock (we would say the "structural ancestry") of such diverse groups as the caenolestids, thylacynes, kangaroos, phalangers and many others, living and extinct.

Paleontologists do not reason that an ancestral stock "passed on a certain group of its characters to each and every one of its descendants," and this statement is a reversal of the logic actually involved. If certain characters are found to be common to all, or even to most, of a group of related forms, it is concluded that these characters probably occurred in the ancestral species. In numerous cases where we have phylogenies of various groups reasonably well sampled by paleontological collections, this has been found to be true in fact, and it is a reasonable generalization from our data. It is not invariable, the exceptions being cases where a character has arisen independently in different lines, but this result can not be confused with a truly common ancestral condition if the data are adequate. As for the fact that transformation does occur and that a given character may be lost or unrecognizably altered in descent, this is so obvious in every phylogeny that it is a paleontological truism, although it is not difficult to find isolated studies in which the possibility has been unduly minimized.

(9) "The number and magnitude of the characters common to any category depends on the age of the category,"—or rather on the rank of the category, for it has

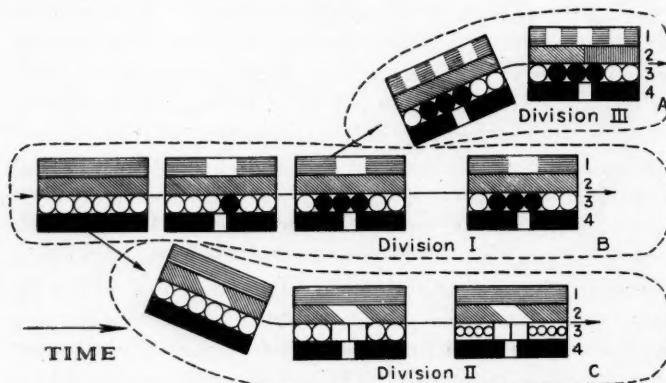


FIG. 10. Distribution of a few relatively more variable (generic and specific) characters in three species derived from a common ancestry. Closely related species, such as any two in succession, or A and B, have more in common than more distantly related species, such as A and C, or the single ancestral species and any one of the terminal species. A and B derived their identical character 4 from their common ancestry. C has developed the same character by parallelism, but its other characters plainly show that it is markedly distinct and less close to either A or B than the latter are to each other. The parallelism would be less close were they farther removed from a common origin. The lines, phyla or branches of species are labeled as Divisions I, II and III. These are natural higher categories. The data also show a two-fold division into natural higher categories, one consisting of Divisions I and III and one of Division II. All three divisions together, the whole diagram, also form a single natural higher category. The hierarchic rank assigned to these different categories depends on other considerations and there is no absolute criterion of rank, but the categories are real.

been shown above that the age criterion is valid only as far as the primary dichotomy leading to a given category is invariably (and obviously) older than dichotomies within the category. In discussing *Henricosbornia* it has been shown that this is not invariably true, and the results obtained in this genus are in remarkably close agreement with those of Kinsey on *Cynips*.⁷ This has been stressed because it is a novel idea in paleontological work in general that "generic" differences may be distributional and not different in kind or intensity from "individual" or

⁷ All the more striking in that they were obtained, and that part of this paper written, before Kinsey's study was published or I was aware of it.

"specific" differences. On the other hand, it still seems that this is novel largely because it is exceptional, and that the principle here quoted is probably valid, even though it has exceptions. These exceptions probably occur only in relatively small categories, say approximately within genera or at most subfamilies, and near the beginning of the differentiation of larger categories, before they have, in fact, attained the higher rank.

It is quite obvious that larger groups eventually differ vastly more than do species, and in different ways. No two species, to take a case that reduces the argument to absurdity, differ either qualitatively or quantitatively in limb structure, as do all perissodactyls and all whales. These differences are no doubt an accretion of small steps, and the first dichotomy that was to lead eventually to whales and to perissodactyls was probably of specific type, but if that is all that this new view-point means, then it is merely repeating in other words what every zoologist has long believed and its attack on current views is meaningless.

It is a valid generalization from all our data that the rank of a category is usually and roughly inversely proportional to the number and magnitude of the characters common to all its members.

(10) "Categorical rank is to be determined by the nature of the particular characters involved." This is correlated with the preceding principle and may be considered in much the same way, as not literally true in this form (or accepted by most zoologists), but as embodying a truth. Examples have already been given of characters that are supra-specific in some groups and infra-specific in others. However often they may have failed in the correct analysis of particular cases, paleontologists have long understood that this is true. The mode of attack is not by an *a priori* assignment of rank to some type of character, but by studying particular groups to discover the ranks of its various characters. Certain characters have been found usually to have supra-specific

rank, and in such cases it is a proper procedure to assume that they will have such rank in other groups, but only unless proved otherwise and with a lively anticipation that the contrary may be true.

(11) "Reproductive organs . . . are more conservative than other structures and, therefore, of greater significance in establishing higher categories." Paleontologists do not ordinarily deal with reproductive organs, but they do have quite analogous parts that are considered as usually more significant in establishing higher categories, for instance, in mammals, the astragalus, enamel histology or the foramina and other characters of the ear region. Sometimes too great reliance on these has resulted in error. Yet all paleontologists recognize in theory and try to involve in their practice the fact that all organs are subject to variation, convergence and all the other confusions for the taxonomist. Some characters have, however, been found usually to vary less than others, and it is proper and valid to stress these in establishing higher categories. Here again, it has not been the practice, as the form of the criticism seems to imply, to assume *a priori* that some particular set of characters is necessarily diagnostic supra-specifically. It is very often found that these more important characters are not the same for different groups. The examples already given of the conservatism of a given set of characters in one suborder of notoungulates while the same set is radically variable in another suborder are sufficient to establish this.

(12) "The adaptive nature of a character determines the categorical rank of the unit in which the character is found." Gregory has discussed this principle, in another form, and has divided characters of any given group into heritage and habitus, the heritage being the older characters, usually not immediately or obviously adaptive to a particular mode of life different from those of the close relatives of the group in question, while the habitus includes characters of more recent origin and often (not

invariably) adaptive in this sense. In general the heritage is diagnostic of higher and the habitus of lower categorical ranks. In paleontological work, however, the adaptive nature of a character is not commonly used as the direct criterion of taxonomic rank, and there are obvious pitfalls in attempting to use this as an inflexible rule. As Gregory has also noted, the heritage of any particular group was commonly the habitus of its unified ancestry.

(13) "The capacity of two groups to hybridize is inversely correlated with their categorical rank." This is not open to direct paleontological proof or discussion. There seem to be no paleontological examples in which hybridization can be positively demonstrated, although it is suspected in a number of cases. In any event, it obviously is not available as a taxonomic criterion for fossils.

This completes the list of current concepts of higher categories that it was proposed to review. In addition to these, two other points may be mentioned because they involve paleontological evidence.

A process that seems to be little stressed in zoological work, and especially in experimental biology, is the disappearance of genetic factors. Kinsey says, "all of the characters that have ever been in the species should be found in at least some of the individuals in any adequate sample of the population to-day." No explicit limitation is made, but perhaps only the genus *Cynips* is intended, and surely this can not be meant as a generalization or to apply to higher categories. It is impossible to believe that all the genetically determined characters of *Hyracotherium*, for instance, still exist in *Equus*. In fact, characters can be lost, as well as acquired, and the loss may give rise to new groups just as truly as does the acquisition. The history of mammals is replete with structural losses—teeth are lost, toes are lost, vertebrae are lost, pigmentation is lost, eye structures are lost. In at least some of these and the many other examples that

could be cited, it seems certain that the genetic determinants of these characters are not merely overlaid by new mutations, but are quite eradicated from the heredity. This, in essence, is the basis of the law formulated by and named for the great Belgian paleontologist, Dollo, the law that a structure once lost can never be regained. Despite apparent exceptions, the law as now interpreted is accepted by all paleontologists as essentially true, and a host of examples are at hand to support it. If loss can and does occur in animal phyla, it must also occur, to some extent, within species, since all evolutionary processes, after all, must affect individuals and all individuals belong to species.

Differential evolution involves the whole animal, and thus different species can arise without much effect on the skeleton (*e.g.*, lion and tiger, which certainly are good species, but which are difficult to distinguish osteologically, or some of the zebras and horses). Theoretically, species might be distinct yet not differ appreciably in any morphological character, but only in some physiological, chemical or perhaps psychological character. Kinsey cites examples of "absolutely indistinguishable" gall wasps which nevertheless consistently produce very distinct galls, hence are by him classed as different species on this physiological basis. I do not know of any such extreme examples among vertebrates, but nevertheless there are mammals that differ in physiology or psychology as much as in morphology. It is reasonable to doubt whether such differences in chemical or nervous activities can really exist without a physical basis, but the physical basis might conceivably be beyond the reach of ordinary morphological research, which may amount to much the same thing as if they did not exist.

Physiological and psychological species of this sort obviously can not be recognized either by the usual taxonomist of recent animals or by the paleontologist, for both work on dead material and whether it died yesterday or five hundred million years ago makes no difference in this

respect. There are also species distinctly different but in characters not preserved in fossils, and these too are beyond the reach of the paleontologist although not of the neozoologist.

These facts undoubtedly help to falsify the details of the paleontological record, but they can not do so to any important extent. If two species do not differ appreciably in morphology, it is certainly true that they are closely related, and an error in supposing them to be one species is not an essential falsification of the general record. It is a principle of paleontological research, and one that so far seems to stand up under the closest scrutiny, that essential structural agreement in any complicated part of animal anatomy implies true relationship. Convergence, the greatest falsifier of records, never produces identity, even in the skeleton alone or even in any considerable part of the skeleton. For instance, some of the South American mammals are very horse-like throughout. They must have looked and acted almost exactly like horses, but they can be distinguished from horses by any single bone in the skeleton and their heritage, the ancient and diagnostic character complex of the group, can be clearly distinguished from the horse-like habitus. Parallel evolution, which is a phenomenon quite different from convergence, even though the two grade into each other,⁸ may produce a much closer and more fundamental resemblance, but even here identity is probably never achieved. No essential falsification of the record is here introduced, for parallelism only occurs among forms that really are related, and in general all the evidence favors the rule that the closer the parallelism, the closer the relationship. It is often difficult to distinguish rather distant parallelism from rather close convergence, but it is unlikely that many gross errors in this respect occur in careful, recent work.

⁸ Kinsey's cases of independent origin of similar characters in *Cynips* seem all to be parallelism, not convergence, properly speaking.

SUPRA-SPECIFIC VARIATION IN NATURE AND IN CLASSIFICATION¹

A FEW EXAMPLES FROM MAMMALIAN PALEONTOLOGY

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IN paleontology the only evidence that any particular group of specimens belongs to a single species is usually that the fossils come from one locality, from a single horizon, and are nearly alike in almost all observable features except those which may be plausibly attributed to differences in age or in sex. When, however, we are comparing specimens from different horizons there are often more or less constant differences to which specific rank is customarily assigned.

When we consider the genera, subfamilies and families of different paleontologists, we find widely different viewpoints and customs. For example, Fig. 1 represents a series of extinct lemuroid primates, described by Cope, Marsh, Osborn, Matthew, Granger and myself. The fossils were found in successive formations in the Eocene of Wyoming. In the oldest one, at the bottom, the first upper molar conforms to what is called the tritubercular pattern, since it has three main cusps. In the specimen at the top, which is the latest in time, the size has greatly increased and the first upper molar has now four main cusps plus a prominent mesostyle on the outer side of the crown. Moreover, the last upper premolar has two outer cusps, instead of one as in the figure at the bottom. The specimens from intermediate horizons show transitional stages from the bottom to the top of the series. Fig. 1 represents only a small part of the entire series, in which there are many intergrading conditions. These forms

¹ Read at a symposium of the American Society of Naturalists in joint session with the American Society of Zoologists, the Botanical Society of America, the Genetics Society of America, the American Phytopathological Society and the Ecological Society of America. The American Association for the Advancement of Science, Atlantic City, N. J., December 30, 1936.

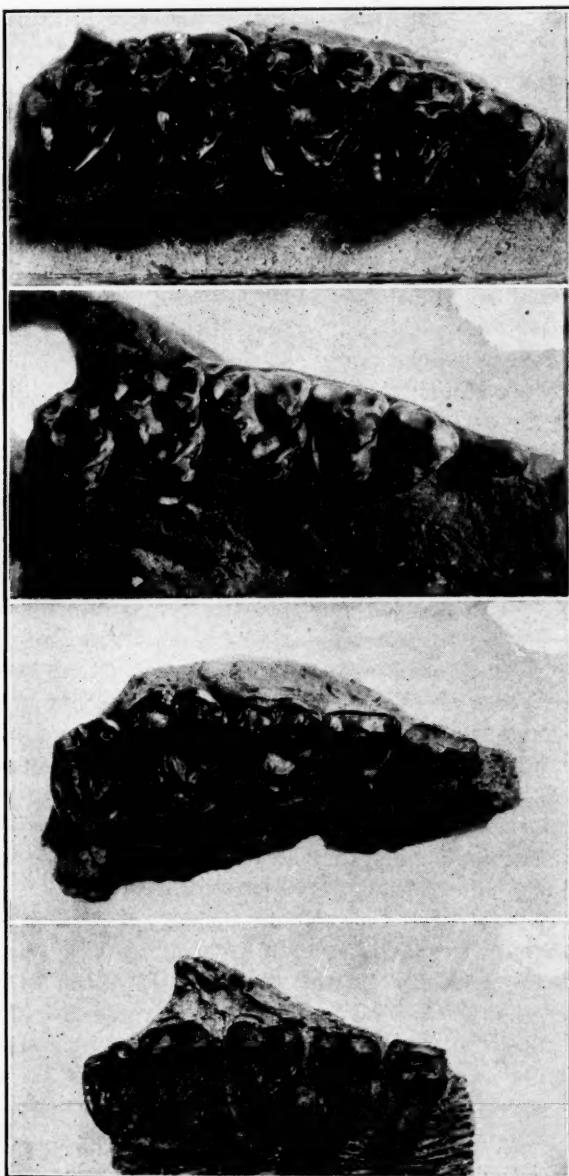


FIG. 1. Synopsis of evolution of the upper molars of Eocene lemuroids.
1.—*Pelycodus ralstoni*. 2.—*Pelycodus jarrovii*. 3.—*Notharctus osborni*.
4.—*Notharctus crassus*. All figures three times natural size.

were discovered at different times and the literature of paleontology records eight nominal genera and twenty-odd nominal species. If we define genera by the so-called horizontal system, we can construct three generic definitions corresponding to the structural stages. If, however, we consider a genus as a phylogenetic succession of species, which was the usual practice of Professor Osborn, then the whole series falls into one genus. In cases of this kind, which are fairly numerous, some paleontologists will make one choice, some another; the result is that in comparing alleged "genera" of different groups or the same generic names as used by different authors, there is but little uniformity. But because the names are different or the customs of authors are different, is the series itself any less illuminating as an actual example of evolution?

Fig. 2 shows the lengths of the three lower molars in a series corresponding to the upper molars of Fig. 1, but including many more specimens. The figures confirm what we can see without measurements, namely, that there is a general increase in size and that at any given horizon some forms are more conservative than others. There is also an evident tendency, when we have a sufficient number of specimens, for the measurements in any given horizon to segregate themselves into groups or clusters, separated by considerable gaps in size from related groups. Such clusters are usually called species by paleontologists and they may often be defined by small but fairly constant morphological differences.

The titanotheres were a family of extinct perissodactyl mammals that ranged in North America from the summit of the Lower Eocene to the top of the Lower Oligocene. Their fossil teeth, skulls and skeletons are described in a monograph on this family by the late Henry Fairfield Osborn.

During this period, which may be tentatively estimated at about ten million years, the race as a whole increased in size from small animals about as big as a whippet hound to giants surpassing the existing rhinoceroses.

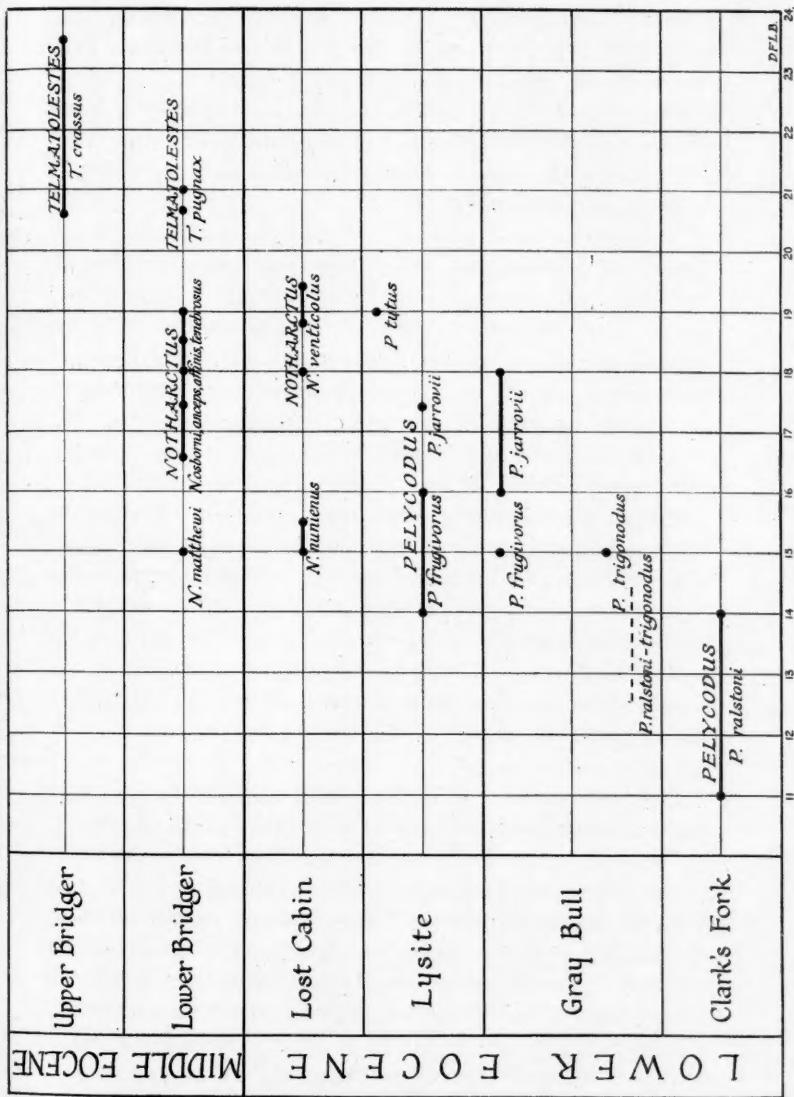


FIG. 2

In the later members of the group paired bony swellings grew up above and in front of the eyes. Meanwhile the upper and lower true molar teeth retained the same general patterns but increased greatly in size.

The second, third and fourth upper premolars, however, gradually became more complicated, changing from a triangular to a quadrangular crown and acquiring a large posterointernal cusp.

In the period of discovery and description of the North American titanotheres, extending from 1846 to 1919, no less than one hundred and fifteen nominal species and thirty-eight nominal genera of titanotheres were given formal names. Considering only the later or Oligocene titanotheres, a few of these alleged species and genera were based on real differences between what are now supposed to be males and females of the same species. Separate species names were also given to the several intergrading stages, ranging from small adult male skulls with small horns to very large horns of flattened cross-section. There was a great deal of parallelism among the later genera with regard to the increasing size of the skull and of the horns, but the different genera may be defined not only by differences in the cross-sections of the horns but also by differences in the premolar and molar teeth and in the proportions of the skull, from very narrow to very wide.

The lower molars (Fig. 3) increased more or less rapidly in length from the oldest to the latest titanotheres.

There are two kinds of genera (so-called) of titanotheres, even in Professor Osborn's monograph. In one case, as in the Middle to Upper Eocene genera *Mesatirhinus* and *Dolichorhinus*, the older and more primitive forms were put in one genus, the later and more advanced forms in another. In the second usage both ancestors and descendants are put in the same genus, as in the various so-called species referred to the genus *Brontotherium*.

In his numerous papers and in the monograph on the Proboscidea Osborn also used the word genus to cover a series of ancestors and descendants, as in his figure of

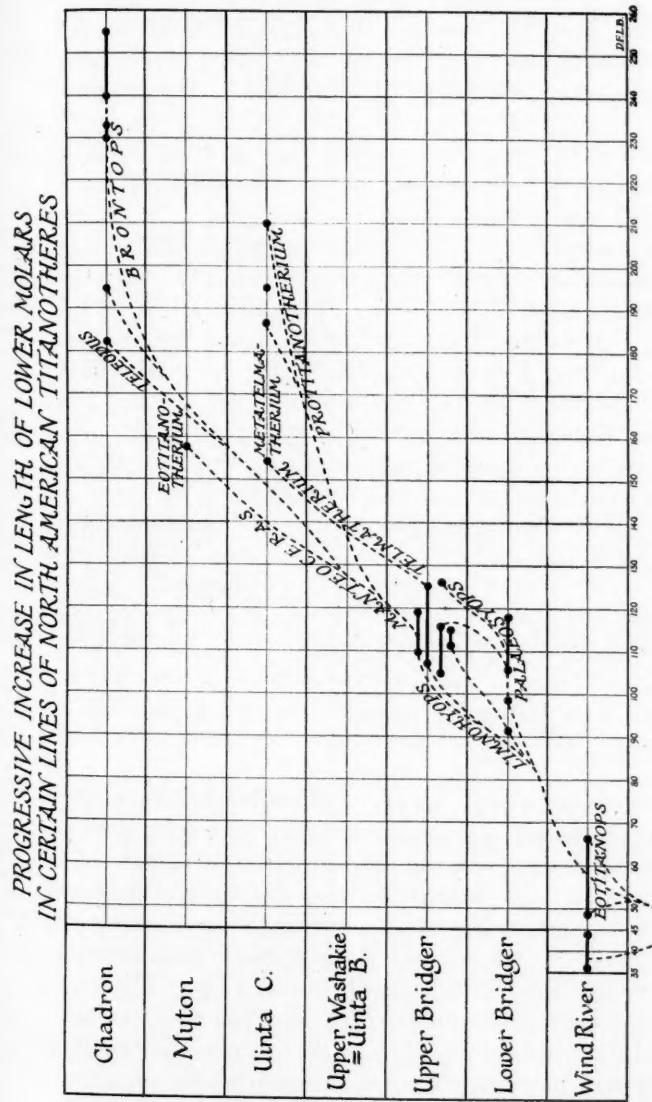


FIG. 3

the molar teeth of the species of "*Trilophodon*." In this so-called genus the number of component units of the molar pattern increased from twenty to thirty-seven during the estimated fourteen million years of the Miocene and Lower Pliocene epochs. This vertical usage of genera and subfamilies by Osborn has not been adopted by other paleontologists and seems like a needless break with well-founded practice.

Next I may refer to a remarkable example of variability illustrated in a series of fossil rhinoceros skulls from the Lower Oligocene of Colorado. The material is in the Colorado Museum of Natural History at Denver and was described in 1928 by William K. Gregory and Harold J. Cook. Although all coming from one quarry and one horizon, literally no two of these skulls are alike, even after we have discounted differences due to age and sex. The most conspicuous variability is shown in the patterns of the upper premolars (Fig. 4). In the most primitive

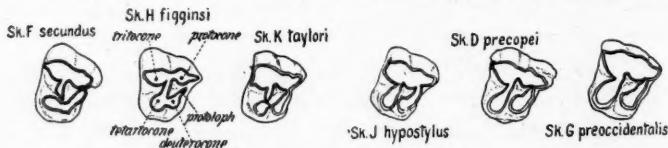


FIG. 4. Second right upper premolars of *Trigonias*, showing range of variations in crown pattern from premolariform to molariform. After Gregory and Cook.

stage the inner side of the upper premolar crowns is more or less V-shaped, the tip of the V being lost in a large round inner cusp. In the most advanced stage the V is broken into two parallel crests. Between these are numerous intergrading stages, during which the posterior limb of the V grows from a small beginning, becomes larger and connects itself with the inner cusp. The latter meanwhile divides itself into two, the fore part going with the anterior cross-crest, the rear part shifting still further to the rear and conjoining with the incipient posterior cross-crest. Eventually the front and rear cross-crests become subequal. The differences between the extremes are such as have been given generic rank among related fossil rhinoceroses.

GRAPH 1. VARIABILITY OF SKULL MEASUREMENTS AND INDICES
 RELATIVE INDIVIDUAL AGE OF SKULL INDICATED
 BY SEQUENCE OF LETTERS

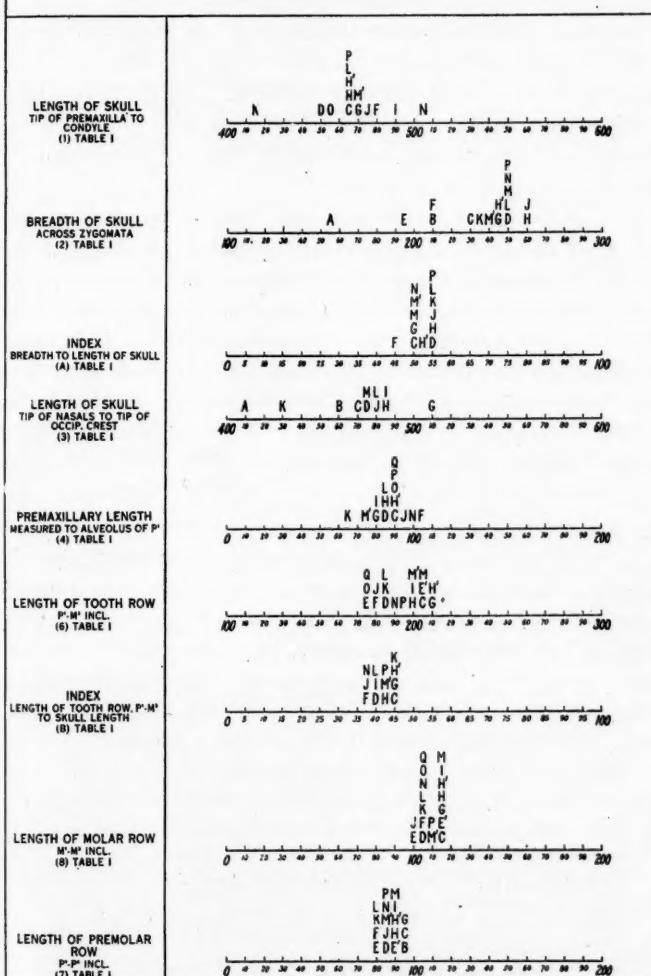


FIG. 5

But in addition to the intergrading conditions in the premolars, we have the highly varying measurements of the skull and dentition. When these measurements are arranged in graphs (Fig. 5) they are seen to conform more or less to the normal curve of variation. If there were more than one species involved the measurements ought to show a tendency to segregate themselves into two fairly distant humps, which in general they do not. The conclusion seems to be that in this case a single variable species includes forms which would usually be referred to two or three distinct genera.

In conclusion, it seems obvious that in attempting to interpret the phylogenetic value of the so-called species, genera, subfamilies, etc., in different groups and of different authors, one must know well, first, his material and, secondly, his authors. Nevertheless, admitting the many inconsistencies and contradictions of diverse usage, my experience suggests that the so-called species and genera do in one or another determinable way represent the successive and contemporaneous twigs and branches of evolutionary history; that these twigs divided dichotomously during geologic time; that the various branches pursue partly divergent, partly parallel and partly convergent paths. The great value of even an inconsistent system of classification is that, when based on a sufficiently broad series of characters, it becomes an indispensable device for symbolizing, however imperfectly, the inconceivably vast and extensive ramifications of the very real tree of life.

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SHORTER ARTICLES AND DISCUSSION

THE INHERITANCE OF THE COLOR OF MALPIGHIAN TUBES IN *DROSOPHILA MELANOGASTER*

In connection with transplantation experiments carried out by Dr. Boris Ephrussi and the writer, it was noted that the larvae of certain mutant stocks were characterized by colorless or pale yellow Malpighian tubes in contrast to the bright yellow tubes of wild-type larvae. A distinction between bright yellow and white or between bright yellow and pale yellow Malpighian tubes can be made by observing living larvae on a black background with a standard wide field binocular microscope with a magnification of approximately 16 diameters.

So far as known, the only genetic types which have white or pale yellow Malpighian tubes are eye color mutants. However, it should be pointed out that the only systematic survey of genetic stocks made has been limited to stocks carrying eye color mutants. It is known that larvae of stocks homozygous for the X-chromosome characters white (*w*), ruby (*rb*), carmine (*cm*) and garnet-2 (*g²*), the second chromosome character light (*lt*) and the third chromosome characters peach (*p^p*) and claret (*ca*) have colorless or very pale yellow Malpighian tubes. Many other eye color mutants have characteristically pale yellow Malpighian tubes, for example, vermillion (*v*, chromosome 1), cinnabar (*cn*, chromosome 2), brown (*bw*, chromosome 2) and maroon (*ma*, chromosome 3). It is of interest to note that larvae of the double recessive stocks *v bw* and *cn bw* have colorless (or practically so) Malpighian tubes.

Two examples of the use to which Malpighian tube colors can be put will be cited. In the first instance, it was desired to identify singed-1 (*sn¹*, chromosome 1, bristle character) females in larval stages.¹ Since singed-1 females are sterile, homozygous stocks can not be used. By making the mating *w⁶sn/CIB* ♀ × *w⁶sn* ♂ (*CIB* designates a particular X-chromosome inversion associated with certain mutant genes of no importance in this particular mating), female larvae could be separated into two classes with respect to Malpighian tube color. Experience made it evident that those with white Malpighian tubes were *w⁶sn/w⁶sn* and those with yellow tubes *w⁶sn/CIB* in constitution. In other words, eosin (*w⁶*, a white allele) was used as a larval character

¹ C. W. Clancy and G. W. Beadle, *Biol. Bull.*, 72: 47-57. 1937.

to mark the chromosome carrying singed. In a similar way, fused (*fu*, chromosome 1, wing veins fused, female sterile) larvae were identified in the mating *w fu/CIB* ♀ × *w fu* ♂. In the second case,² Malpighian tube color was used to identify super-female larvae (3X, 2A). From the mating attached-X white ♀ × wild-type ♂ (essentially but not actually this mating was used), three types of zygotes are expected: *w/w* + ♀♀ (XXX), *w/w* ♀♀ (XXY), and + ♂♂ (XY). Of the females, the super-females have yellow Malpighian tubes, the diploid females have white tubes. The above examples show that white Malpighian tubes differentiated from wild-type by the white gene segregate into a readily distinguishable class.

In an attempt to build up a balanced stock of female sterile (*fes*, chromosome 2, ovaries rudimentary) in which homozygous *fes* females could be identified by Malpighian tube color,¹ *fes lt/Cy* (*Cy*, Curly wing, chromosome 2, associated with inversions) was tried. It was found that from the mating *fes lt/Cy* ♀ × *fes lt* ♂, all offspring had yellow Malpighian tubes. Since this result differs from that obtained with white and eosin, a further investigation of the white Malpighian tube character associated with light eye color was made. The following matings were made involving *lt*:

+ (Ore-r) × *fes lt/Cy, al lt*^m *L*¹ *sp*²
*lgl sp*² × *fes lt*
*lt × lgl sp*² × *Cy*
lt × + (Swed-c)
+ (Swed-c) × lt

In all cases the *F*₁ larvae were examined and found to have yellow tubes. The following back-crosses, using heterozygous *lt* females, were then made (maternal chromosome given first in female constitutions):

Cy/fes lt × fes lt
*lgl sp*² × *fes lt × fes lt*
lt/Cy × lt
lt/+ × lt
+/lt × lt

Examinations of the larvae from these matings showed that in all cases all larvae had yellow tubes, but there was considerable variability in color. Samples of larvae with dark tubes (total 28) were segregated from those with pale tubes (total 33) and grown to maturity. Those with dark tubes gave 27 adults with wild-type eye color and one with light eye color; those with pale tubes gave six adults with wild-type eye color and 27 with light

² G. W. Beadle and B. Ephrussi. Unpublished.

eye color. It is evident that a partial separation of wild-type and light was made on the basis of Malpighian tube color. When light flies from the above crosses were mated among themselves, the resulting offspring all had white larval Malpighian tubes.

From the back-crosses in which light flies were used as female parents:

$$\begin{aligned} lt \times lt/Cy, \\ lt \times lt/+, \text{ and} \\ lt \times +/lt \end{aligned}$$

the results were quite different; the larvae could be readily separated into two classes, one with white tubes, the other with yellow tubes. Of 105 larvae classified, 54 had yellow and 51 had white Malpighian tubes. A total of 58 larvae were separated on the basis of Malpighian tube color and grown to maturity. Thirty larvae with yellow tubes gave rise to adults with wild-type eye color, while 28 with white tubes all gave larvae with light eye color.

It is evident from the above experiments that genetically *lt* larvae from heterozygous *lt* mothers have yellow Malpighian tubes, while larvae of identical genetic constitution from *lt* mothers have white tubes, and that we are therefore dealing with a case of maternal influence. It is of some interest that of the two characters associated with the *lt* gene, Malpighian tube color shows a maternal influence under certain conditions, while eye color shows no evidence of such an influence. This may be related to the fact that Malpighian tube color appears very early (before egg hatching, according to Poulson³), while eye color does not appear until relatively late in pupal development.

From the fact that many genes associated with eye color characters in *Drosophila* are likewise associated with modifications of Malpighian tube color, there is reason to suppose that the two pigment systems are rather closely related developmentally. This supposition receives some support from certain transplantation experiments reported elsewhere.⁴ Similarly, there are reasons for supposing that testis sheath color is likewise rather closely related developmentally to eye and Malpighian tube color (see Dobzhansky⁵).

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³ D. F. Poulson, *Actualités Sci. et Indust.* In press.

⁴ G. W. Beadle, *AMER. NAT.*, 71: 120-126. 1937.

⁵ Th. Dobzhansky, *Roux' Archiv. f. Entw.-mech.*, 123: 719-746. 1931.

SECOND RECORD OF RARE FRESH-WATER
JELLYFISH FOR MISSOURI

ON September 6, 1931, a single male medusa, 10 mm in diameter, was found near St. Charles, Missouri, by Michael S. Wepprich, Jr., a student at that time at the University of Missouri. The specimen was identified as *Craspedacusta ryderi* (Potts), was the fifteenth American record and the first Missouri record.¹

On August 20, 1936, the writers collected six specimens of medusae of several dozen observed in the warm water of a quiet, clear, rock-margined pool of porphyritic trachyte rock along a "shut-in" of Marble Creek in Sect. 21, T. 32N., R. 5E., near Fredericktown, Missouri.

The writers identified these specimens as *Craspedacusta sowerbyii*. Dr. Fernandus Payne, of Indiana University, who confirmed the identity of the two specimens sent him, found them to be males. In correspondence with Dr. Payne regarding these specimens, the fact was brought out that in his earlier paper on *Craspedacusta* the specific name of *ryderi* was given, because it was his belief at this time that this was not the same species as described in England under the name of *sowerbyii*. This distinction was based on the life history which had been worked out by Dr. Payne in Indiana. The two life histories were different; however, the structure of the adult medusa appears to be the same.

Of added interest is the fact that found in the same creek with the medusae occurred a species of a colorless green alga belonging to the genus *Enteromorpha*, this species being one of a few fresh-water species of an otherwise marine genus. This association and occurrence of two fresh-water forms of otherwise salt-water plant and animal groups may indicate that these present fresh-water forms may represent relict or surviving types in a region which may formerly have had a more or less direct connection with salt- or tidewater in past geological history of the region, as, for example, when the Mississippi Embayment in Tertiary times penetrated southeastern Missouri.

Apparently the North American specimens of the fresh-water medusae so far reported should be assigned to the genus *Craspedacusta* Lankester, with the specific name *sowerbyii*.

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JULIAN A. STEYERMARK

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CONTRIBUTIONS TO THE STUDY OF EVOLUTION:

I. TEMPORARY HEREDITY AND THE MECHANISM OF ADAPTATION

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ALL biologists agree that the vast majority of species, both animal and vegetable, display structural and functional peculiarities which adapt them to the environment in which they live. In many cases these adaptations are very similar in kind to the modifications which individuals of other species acquire if placed in the same environment, but they are much greater in degree and they appear to be inherited. The native man in the tropics, for instance, is dark-skinned, and his pigmented skin is inherited, but the white man who moves to the tropics displays an individually acquired character of a similar nature—he becomes sunburned. One of the great unsolved problems confronting biology concerns the manner in which these adaptations arose. Did they originate through natural selection, which perpetuated those minute individual variations most suitable to the environment? Or did they arise through an individually acquired character becoming hereditary? In the illustration already referred to, did the dark-skinned races originate through the weeding-out of the paler and the perpetuation of the darker among the individual variations in pigmentation of the skin, or did the individually acquired character of becoming sunburned in the tropics become hereditary? There appears

to be a rather strong consensus of opinion to the effect that acquired characters can not be inherited, or at least that any experiments designed to prove that they can be inherited only yielded very unconvincing results. But, on the other hand, many species become acclimatized to a new environment very quickly—that is, they become adapted to the new climate—so quickly in fact that it is difficult to conceive of the process being wholly due to natural selection acting on slight individual variations. Davenport (1907), for instance, considers that the process of acclimatization is too rapid to be solely due to natural selection and too slow to be due to each generation successively acclimatizing itself. He therefore concludes that there is some transmission of acquired acclimatization. We appear therefore to have reached a deadlock. Some facts point in one direction, others in the opposite direction, and we have no certain answer to many of our problems. The real crux of the difficulty lies in the problem whether acquired characters can be inherited in any degree. If we could obtain a definite solution to this question, the ground would be clear for further research.

To some extent the conflict of opinion on these questions arises from the different spheres of different workers. The field workers in general believe that acquired characters can be inherited in some way, though they may be unable to produce a concrete and observable case in support of their contention. For instance, Annandale (1924) in a recent paper states:

My explanation of the phenomena discussed in this paper implies an acceptance of the doctrine of the survival of the fittest and at the same time a firm belief in the inheritance of one kind of acquired character. The traumatic injury of an individual can probably not affect the race, but unless we assume that the long-continued and gradual influence of environment can do so, it is difficult to see how adaptive characters can ever have arisen. The very existence of such characters may be denied by observers in a laboratory or a garden-plot, but in tropical nature they are continually being forced on the notice of the field zoologist. I will cite only two instances which seem to me by themselves sufficient, *viz.* (1) that of the fishes of the genus *Garra* or *Discognathus*, in which we find the most perfect and the most gradual transi-

tion in correlation with environment from forms structurally adapted for browsing on a muddy bottom to forms profoundly modified for life in the rapid-running waters of mountain torrents; and (2) the parallel instance of the Ranid tadpoles which inhabit the same torrents.

On the other hand, the laboratory workers deny the possibility of an acquired character being inherited. They point with some justice to the absence of any convincing experimental proof of such inheritance. Conklin (1930) sums up their conclusions on this question as follows:

(1) Developed characters, whether "acquired" or not, are never transmitted by heredity, and the hereditary constitution of the germ is not changed by changes in such characters. (2) Possibly environmental stimuli acting upon germ cells at an early stage in their development may rarely cause changes in their hereditary constitution, but changes produced in somatic cells do not usually, if ever, cause corresponding changes in the hereditary constitution of the germ cells. (3) Germ cells like somatic cells may undergo modifications which are not hereditary: if starved they may produce stunted individuals and this effect may last for two or three generations; they may be stained with fat stains, and the generation to which they give rise be similarly stained; they may be poisoned with alcohol or modified by unusual temperature and such influence may be carried over to the next generation without becoming permanent. All such cases are known as "inductions" and many instances of the supposed inheritance of acquired characters come under this category. (4) Environment may profoundly modify individual development, but it does not generally modify heredity. (5) There is no conclusive evidence that the effects of training are inherited through the germ cells.

We are therefore faced with a very wide divergence of opinion on this question. The field workers present us with facts which are difficult to explain except on the assumption that acquired adaptations can be inherited. This, however, does not constitute proof that acquired characters are inherited, for quite possibly some other explanation may be forthcoming that will explain such cases. The laboratory workers, on the other hand, argue from the absence of decisive evidence in favor of such inheritance and from the fact that many experiments specially designed to prove the inheritance of acquired characters yielded only negative, or, at least, very unconvincing results. It should perhaps be stated in parenthesis that this division of workers into field and labora-

tory is very arbitrary and not accurate, for many workers are active in both spheres, but it is useful as a means of representing two points of view, the one reasoning from observations of facts in nature, the other from the results of experiments.

On the whole, the laboratory workers, basing their conclusions on experiments, appear to have the stronger case, but their views are colored to some extent by the Weismann theory, which in general is accepted by them. But, while the Weismann theory may be useful as a broad generalization, no conclusive proof of its absolute truth has ever been obtained, and many modern workers would dispute its correctness. They point out the impossibility of demonstrating the existence of a perpetual distinction between germ-plasm and somato-plasm in plants, and, as the phenomena of inheritance are so closely similar in both animals and plants, we are compelled to acknowledge that the mechanisms underlying these phenomena are almost certainly the same in the two great kingdoms of living organisms. When therefore the laboratory workers or geneticists, arguing from the Weismann theory, point out that we can not explain how an acquired somatic character can affect the germ-plasm, their objection should really carry no weight. The fact that we can not explain how a thing occurs is no proof that it does not occur. The Weismann theory may not be true, or it may require amplification in such a way as will make such possibilities understandable. In approaching these problems therefore we need to avoid prejudicing the matter by making assumptions that we can not defend. The fact that we can not explain how adaptations have arisen unless we assume the inheritance of acquired characters is no proof that such inheritance does in fact occur, and the fact that we can not explain how modifications of the somatic cells affect the germ cells is no proof that such an effect does not occur. We need first to ascertain exactly what facts do occur and then if we wish we can devise theories to explain how such facts are possible.

By an inherited character biologists or geneticists mean one that arises independently of the environment in which the individual is placed. Such a character, in some cases, may be a capacity to respond to a certain environmental stimulus, and will not manifest itself unless the necessary stimulus is present. But the capacity to respond to that stimulus is always present regardless of the environment. For example, green plants inherit a capacity to develop chlorophyll in the presence of light and a trace of iron. If either light or iron is absent from the environment this capacity can not be exerted, but the capacity is always there, no matter what the environment may be, and all green plants in the presence of light and iron will produce chlorophyll. New characters sometimes arise, apparently by changes in the hereditary constitution of the germ cells due to unknown causes. These are called mutations and are always fully developed from their first appearance, and are not altered by the environment. We can not regard them as being, in any way, adaptations to a new environment. One of the characteristics of an inherited character is that, as far as we know, it can never be destroyed or completely disappear, except possibly by mutations arising in the germ cells, in which case it will disappear suddenly and completely. One character, if it is recessive to another, may be concealed for countless generations, but it is always present in the germ cells, and if in the process of fertilization two germ cells, each bearing the recessive character, happen to meet, the character will appear again. For example, a red coat is a recessive character in Aberdeen-Angus cattle, and in all herds an occasional red calf occurs. Hereditary characters therefore are permanent, or rather persistent, and they obey the Mendelian laws of heredity.

The object of this paper is to suggest that there is a considerable amount of evidence which supports the view that another type of heredity exists, which is concerned not with actual visible characters but with the capacity of the organism to respond to new stimuli in its environment.

An organism can become attuned to a stimulus and this attunement apparently can be inherited and enables the next generation to respond more easily to the same stimulus. Further, this attunement to a stimulus appears to be inherited in a temporary manner only; it both appears and fades gradually and not suddenly as in mutations. I therefore propose to call this form of inheritance temporary heredity to distinguish it from the ordinary permanent heredity mentioned above. It also would appear to be uncertain whether capacities inherited by temporary heredity obey the Mendelian laws. But they seem to be quite distinct from the inductions mentioned by Conklin.

A question to which a great amount of attention has been directed, and to solve which many experiments have been tried, is whether immunity to a given disease is inherited or not. Hill (1934) published a very useful review of the literature on the subject. Some species are completely immune to strains of bacteria that are extremely pathogenic to other species, and these specific differences are undoubtedly inherited. But these experiments are more concerned with the differences in immunity displayed by different strains of the same species, and with the immunity that individual members of a species acquire in consequence of an attack by a given disease or of injection with a given strain of bacteria.

Webster (1925) carried out the following experiment: A strain of mice from the Rockefeller Institute was taken. After they had borne litters, the latter were weaned and the parents were infected with the mouse typhoid bacillus. Sixty-six per cent. of them died. The litters from the first six parents to die were selected, and when they had produced litters and weaned them they in turn were injected with mouse typhoid. The litters of the first six to die were again selected, and the process was repeated for four generations. In each generation a control stock of unselected mice from the same strain was also inoculated to check the virulence of the bacteria.

The following mortality rates were obtained in the different generations of selected mice:

	Mortality rate per cent.
Parents from original stock	66
F1	50
F2	80
F3	85
F4	71

From these figures it would appear that high susceptibility to mouse typhoid is inherited, but selection over several generations does not lead to a marked progressive increase in the degree of susceptibility. It is important to note that the susceptibility of the offspring could not in any way be dependent on the fact that their parents had been inoculated with the disease, for in each generation they were born and weaned before their parents were infected.

At a later date Webster (1933a) repeated these experiments on a larger scale. He again took a strain of Rockefeller Institute mice, 500 females and 100 males, and mated them. After the young were weaned the parents were injected with *B. enteritidis*. If both parents died within ten days the progeny were selected as susceptible and were mated brother to sister. If both parents survived, then the progeny were injected. If all the progeny survived, their parents were tested twelve times for the presence of the bacterium in their stools, and if all these tests proved negative a further litter was obtained from them and selected as a resistant strain. These were then mated brother to sister. The further selection of these two stocks was based entirely on the reaction of their offspring. Two litters were obtained from each animal, and these litters were tested. In the susceptible stock the parents were rejected if their litters showed a mortality rate of less than 80 per cent.; in the resistant stock the parents were rejected if their litters showed a mortality rate greater than 20 per cent. If the reactions of the first two litters were satisfactory, a third litter was obtained

from the parents and used to carry on the line. The susceptible line was carried on for six generations and the resistant for four.

It is important to note the difference in the mode of originating these two lines. In the susceptible line the original parents were not infected before the litter from which the line was obtained was born. In the resistant stock the original parents were infected before the litter from which the line was obtained was born. This is a fundamental difference, for, if acquired characters can be inherited, the acquired immunity of the original parents of the resistant line, arising from their injection with the bacteria, might be transmitted to their offspring. Other possibilities also arise which will be mentioned later and which might have considerable influence on the offspring of the original parents of the resistant line in consequence of the parents' having been injected with the disease before the birth of their offspring.

The resistant lines did not show any marked progressive increase of resistance in the successive generations. In the first generation of offspring the mortality rate did fall rather abruptly in most cases, but in the following generations it varied widely, though it seems to have fluctuated about a mean. The following are the actual results.

	Mortality rate per cent.		
	Line 1	Line 2	Line 3
Original stock	37.40	37.40	37.40
F1	16.00	32.35	16.60
F2	9.00	20.00	66.60
F3	15.20	10.10
F4	17.80	15.50

The susceptible lines, though varying widely, did show on the whole a progressive increase of susceptibility. Following are figures obtained for all lines taken together.

	Mortality rate per cent.
Original stock	37.4
F1	60.9
F2	65.7
F3	82.3

The results of these experiments suggest that selection of resistant lines does not lead to any increase of resistance—in fact, after a couple of non-infected generations have elapsed the resistance shows a tendency to fall; but in the susceptible lines selection appeared to lead to a progressive increase of susceptibility. The original parents of the susceptible lines had not been infected before the line originated, and as both resistant and susceptible lines were kept very carefully out of contact with possible infection we can say that these experiments suggest that in a stock kept completely free from infection for some generations resistance appears to decline. This tendency may of course have been hastened by selection in Webster's susceptible lines and slightly retarded by selection in his resistant ones.

Manresa (1932) carried out experiments on rabbits along rather similar lines. Litters were obtained from several does and after they were weaned their mothers were inoculated with *B. abortus*. If the mothers produced at least one living young at full term she was classed as resistant; if she aborted or produced only dead young at full term she was classed as susceptible. The pre-inoculation litters obtained from these does were then mated brother to sister and, after they had produced young, were tested. Their pre-inoculation offspring was again selected on their parents' response and so on. The results of these experiments are given in a complicated form, but in general the susceptible lines, to quote Manresa himself, "consistently produced susceptible progeny." The resistant lines showed a "high percentage of resistant animals," but the resistance was not increased by selection and in fact appeared to diminish slightly in the later generations.

Lesné and Dreyfus-Sée (1928) carried out similar experiments and used the same technique as Webster. The time elapsing between inoculation and death was used as

a criterion of high or low resistance. If the parents died within from 24 to 29 hours, their offspring were taken as susceptible; if they died between the 40th and 46th hours, the offspring were taken as resistant. After these offspring had themselves produced litters, they were tested. The experiment was carried on for five generations, and in the fifth generation all the resistant line died between 48 and 80 hours after inoculation, and all the susceptible line died between the 18th and 22nd hours. There appears therefore to have been a very slight increase of resistance in the resistant line and a rather more marked decrease of resistance in the susceptible line. The authors give no actual figures and controls were apparently not used.

These experiments throw no light on the origin of variations. The manner in which they were carried out excluded the possibility of an acquired immunity being transmitted to the offspring, for the parents were not allowed to acquire the character till their young had been born and weaned. Of course the first generation of offspring in the resistant line in Webster's second experiment was exceptional in this respect, and it is noteworthy that the increased immunity of this line persisted for some time. Variations, therefore, or rather further progressive variations, could only arise by mutations, and from these experiments we are led to think that such mutations are rare or of very slight amount. They are so infrequent or so small that the different selected lines did not display any rapid alteration of resistance to the bacterial strain.

Experiments of rather a different kind were carried out by Lambert and Knox (1928) and by Lambert (1932a). They took 220 White Leghorn fowl and injected them with the bacillus of fowl typhoid. Forty-seven per cent. of them died. The survivors which had shown the least clinical reaction were selected, bred from, and the process repeated in the next generation. This was repeated through five generations with the following results:

	Mortality rate per cent.
Original parents	47.7
F ₁	39.8
F ₂	29.3
F ₃	15.4
F ₄	15.0
F ₅	9.4

In a control stock the mortality rate varied from 83 to 89 per cent.

This experiment did result in a progressively lowered death rate. But it is important to realize the difference between this experiment and those described earlier in this paper. In Lambert's experiment the parents of each generation were injected with the disease before the new generation was born or, to be more accurate, before it was laid. At first sight this result suggests the inheritance of an acquired character, but before we can arrive at such a conclusion several possibilities must be considered—possibilities which may also have had an effect on the resistant line in Webster's second experiment mentioned above.

First, we must be sure that all the deaths in each generation were in fact due to fowl typhoid. There is very little doubt that this was the case, for bacillary examinations were carried out on 239 chicks which died during the course of the experiment.

Secondly, we must be sure that the virulence of the strain of bacteria used was kept at a constant level and that the falling death rate was not due to a loss of virulence in the bacteria. Elaborate precautions were taken to secure a bacterial strain of undiminished virulence, and the strain used was constantly tested by injecting controls and noting the mortality rates.

Thirdly, as the chicks in each generation were inoculated when only seven days old, we have to consider the possibility of a passive immunity having been passed to them by their mothers. It is well known that in mammals some of the substances in the blood of the mother which render her immune to certain diseases can pass into the blood of the foetus and render it immune to the same diseases for a

short time after its birth. This is called passive immunity, because the new-born individual does not itself produce the substances conferring protection and this passive immunity generally disappears in the course of a few months. We do not appear to have any certain information as to whether passive immunity can be transferred in fowl from the mother through the egg to the chick. Experiments carried out by Lambert showed that the increased resistance could be conveyed by either parent and it is admitted that passive immunity can not be conveyed by the male germ cell. Besides, a transference of passive immunity would not account for the progressive fall in the death rate.

Fourthly and finally, we have to consider the possibility of the parents' retaining the infection after inoculation and passing it on to their chicks through the egg in such small doses that no pathological phenomena were produced in the latter, but they were stimulated by these minute doses to acquire an active immunity for themselves. This seems to be a rather remote possibility, especially in poultry raised by incubators and having no actual contact with their parents, and again it would not apparently account for the progressive fall in the death rate. Lambert also carried out experiments which seem to demonstrate that this possibility can be safely excluded. He crossed cocks of the selected resistant strain with hens of an unselected strain and also carried out the reciprocal cross. The offspring resulting from the selected cocks and unselected hens did show a very slightly greater mortality rate than the chicks resulting from the reciprocal cross. Now it is generally admitted that, though infection and consequent active immunity may possibly pass from the father to the mother and thence to the egg, yet such a transference is less likely to occur than a transference of infection direct from an infected mother to the egg. As Lambert's experiments resulted in chicks of almost identical mortality rates arising from the reciprocal crosses, it seems highly probable that direct transmission of infec-

tion from mother to chick through the egg does not often occur. Further investigations by Lambert (1932b) showed that 21.3 per cent. of the infected birds became carriers and the ovary was the organ in which the bacteria were most commonly found. This at first sight suggests that probably the infection was passed direct to the ovum or the presence of the bacteria in the ovary directly affected the germ cells. But on comparing the offspring of carrier and non-carrier hens it was found that the latter actually had the higher resistance to the disease.

Gowen and Schott (1933) carried out some ingenious experiments bearing on this question of transferred immunity. They had a strain of "Sil" mice that were completely susceptible to *B. aertrycke*, and a strain of Schwing albino mice that were partly resistant. The two strains differed in coat color, so that they were easily recognized and their hybrids could also be distinguished. If a Sil female is mated in the same oestrus cycle to two males, one a Sil and the other an Albino, she may have pure Sil and hybrid offspring in the same litter. Six double matings were carried out and produced 21 pure Sils and 15 hybrids. When the offspring were sixty days old, they were inoculated with *B. aertrycke*, with the result that all the pure Sils died but only about 53.3 per cent. of the hybrids succumbed. If the immunity of the Schwing albino was due to an actual transference of the infection from the mother to the offspring *in utero*, it should have disappeared in the Sil-Schwing hybrids generated in a Sil uterus, but actually it persisted.

Moreover, the results of Lambert's experiment given above do not stand alone. Hill quotes Roberts and Card (1926-27), who had inoculated 335 day-old chicks with *B. pullorum*. Fifty-three chicks survived and were used to breed a new generation, which was injected and showed a lower death rate. From the survivors of this generation, a third was bred, and when injected in turn showed a still lower mortality rate. Here again we have a progressive lowering of the rate.

Irwin (1929) experimented with rats, using the Danysz bacillus and breeding from the survivors of the infection. He obtained the following results:

	Mortality rate per cent.
Original stock	84.7
F1	42.3
F2	32.6
F3	35.0

He noticed that many of the members of the F2 and F3 generations were undersized, which he attributed to the rather intensive inbreeding which had been practised with the lines. He therefore divided the members of these two generations into those above 65 grams in weight and those below. When this was done the percentage mortality rates were as follows:

	Above 65 gm	Below 65 gm
F2	23.5	50.0
F3	15.3	66.7

This experiment therefore yielded similar results to those of Lambert, but the result was slightly modified apparently by the effects of inbreeding.

Schott (1932) carried out similar experiments on mice, injecting them with *B. aertrycke* and breeding from the survivors. He took great precautions to ensure that the virulence of the bacterial strain used was maintained at a constant level. The following results were obtained in different generations:

	Mortality rate per cent.
Original parents	82.3
F1	64.5
F2	45.8
F3	39.8
F4	36.3
F5	32.6
F6	24.7

Here again an exactly similar result was obtained. In order to test the modifying effect of inbreeding Schott carried out two further experiments. He used the same

technique on two separate lines, each of which was intensely inbred during the course of the experiments. The following results were obtained:

	Mortality rate per cent.	
	Line 1	Line 2
Original stock	53.3	51.0
F1	41.3	49.2
F2	46.0	32.7
F3	31.5	42.4
F4	31.9	35.7
F5	24.7

The results, in general, confirm those of the other similar experiments and they also suggest that inbreeding has a modifying effect in the experiments, as was suggested by Irwin.

Webster (1924b, 1925) also experimented with mice, inoculating successive generations with mouse typhoid and breeding from the survivors. The mortality rate of the original stock was 76 per cent. In the next generation it fell to 42 per cent., and in the next to 15 per cent. But in the third generation it rose to 50 per cent., and for some reason the fourth was not tested. The fifth generation had a mortality rate of 55 per cent. Webster himself states that many of this generation were "puny, under-weight, cold and sickly . . . that some disturbing element had appeared was evidenced by the mortality rate thereafter." Of course the immunity of a stock to a disease depends upon the general health of its members as well as upon their specific resistance to that disease, and if their general health declines, the results of the experiments become valueless. Further, if the fourth generation was not tested, the fifth can not have been bred from survivors and therefore can be completely ignored. It is perhaps remarkable that in view of the obvious sickly condition of the fifth generation their mortality rate did not nearly attain to that of the original parents of the stock. This must indicate that the experiment had resulted in raising the resistance to that particular disease very considerably.

Webster repeated this experiment with a slight variation. He bred from individuals which had survived *two* inoculations of mouse typhoid bacillus and also a lethal dose of mercury bichloride, and when their offspring was tested the mortality rate was only 24 per cent. A control sample tested at the same time had a mortality rate of 70 per cent. It is very significant that the offspring of survivors of two inoculations displayed an appreciably lower mortality rate than the offspring of survivors of a single inoculation.

It appears to be highly probable that in each of these experiments we are not dealing with variations in the general health but with a specific resistance to a particular strain of bacteria. That is, we are not killing off the most delicate members in each generation and breeding from the most healthy, but we are dealing with a particular type of resistance which, though of course influenced by the general health, can be acquired by any individual. Webster (1924a, 1924b) did indeed assert that mice rendered immune to one type of bacteria also showed an increased resistance to other types, even to those not antigenically related to the first type, and even to certain inorganic poisons. But a later experiment by the same author (Webster, 1933b) yielded rather contradictory results, and Topley, Wilson and Lewis (1925) obtained different results. The weight of evidence therefore suggests that in these experiments we are dealing with a specific and not a general immunity. Besides, the difference in the results obtained in the two series seems to exclude completely the possibility that the progressively falling death rate obtained in the second series arose from an elimination of the most delicate members of each generation, for if so the first series of experiments should also have resulted in a falling mortality rate.

We have here then two series of experiments, and the contrast between the results obtained in the two is very striking. In the first series breeding was carried out from individuals of either low or high immunity to a given disease, and before the birth of each new generation no stimulus was applied to its parents which would tend to

increase their immunity. In this series selection either did not result in any increase of immunity or, in one case, brought about a very doubtful and very slight increase, but selection for susceptibility did result in some cases in an increase of susceptibility. In the second series before the birth of each new generation a stimulus was applied to their parents which would increase their resistance, and in each successive generation we find a progressive fall in the mortality rate. In fact, we do not appear to have any record of any experiments in which successive generations were infected with some specific disease and the survivors were bred from, which did not result in an increase in the resistance of the later generations, provided the experiment was persisted in and extraneous influences guarded against. Essentially therefore in the first series the lines were bred in an environment which did not contain the stimulus tending to produce the variation, while in the second series the environment did contain this stimulus.

The results of these experiments, and especially the marked contrast between the results of the two series, apparently compel us to admit that some part of the effect of an infection in the parents is transmitted to the offspring. Of course, a bacterial infection, such as was used in these experiments, generally affects the whole body, and therefore we can understand its having an effect on the germ cells. Possibly such an infection stimulates all the cells of the body to produce their own immunity, and therefore the germ cells would be immune as well as the somatic ones and might pass their immunity to all the cells of the new generation. But this does not appear to be the way in which the germ cells are affected. We have reason to think that the immunity-conferring substance is not produced in the germ cells. For instance, Topley and Wilson (1929) state:

Taking the data as a whole, the conclusions to be drawn do not seem to be in any doubt, in spite of minor discrepancies. There is ample evidence that the organs and cells, which have been shown to be concerned with the clearing mechanism of the tissues, are also concerned in some way with the generation of the sensitizing antibodies. There is no clear evidence that any other organ, or tissue, plays a similar rôle.

By "organs concerned with the clearing mechanism of the tissues" the authors mean what is generally called the reticulo-endothelial system and the lymphocytes, of which the germ cells do not form part. Moreover, we know that in human beings a mother may be immune to diphtheria, but her germ cells do not appear to be immune. Some of the immunity-producing substances in her blood can pass to the blood of the foetus and confer on it a brief passive immunity. But in a few months this passive immunity disappears and the child is not then immune, though it may develop immunity later in life. The effect produced on the germ cells of the parents by the infection in these experiments must therefore be more than a mere capacity to produce their own immunity and the transmission of this character to the body cells of following generations. What effect of the infection in the parents then can be inherited by their offspring?

On what does the immunity of an individual to a given disease depend? The bodies of all animals possess mechanisms by which most strains of bacteria are kept out. The body temperature and the ability of the phagocytic cells to ingest and remove foreign particles, for instance, are parts of this general defence mechanism. The majority of bacterial strains can not combat these defences, and so are harmless. But some bacteria attain an ability to grow at the body temperature, and, even further, they may produce powerful toxins which can paralyze the normal defence mechanism of the host, and these become pathogenic, or disease-producing, to that host. When a strain of these pathogenic bacteria is introduced into the body of a susceptible animal, the latter reacts by producing antitoxins, substances that will neutralize the bacterial toxins and also substances that will have a destructive effect on the bacteria themselves or assist the phagocytic cells to ingest them. These substances are collectively known as antibodies. If the host can produce the antibodies quickly enough and in sufficient quantity, the bacteria will be destroyed and the host re-

cover. But if the host can not produce the antibodies with sufficient promptitude, the bacteria win and the host dies. To say that one individual has a higher immunity than another to a given type of bacterium therefore means that his reaction to the invading bacteria is quicker and more efficient, and he produces antibodies with more speed and perhaps in greater quantity.

In the experiments that we have been considering immunity has been measured by the mortality rates—that is, we really measure the number of individuals in which antibodies are produced quickly enough and in sufficient quantity to save their lives. But most probably all the individuals, even those which died first, reacted to the injection of bacteria by producing or endeavoring to produce antibodies—only they did not produce them in sufficient amount or with sufficient promptitude. And among the survivors the degree of illness produced by the bacterial invasion probably varied considerably—that is, the speed and efficiency of their reaction to the bacteria also varied but in all cases were high enough to save them from death. By using the mortality rate as a measure of immunity, therefore, we are taking one point on the immunity scale and tabulating our results according as they fell on this or that side of the selected point. But the capacity to react to the bacterial infection is present in all the individuals in varying degrees. Our results merely measure a certain magnitude of this capacity. We need therefore to keep clearly in mind that, if our experiments prove that something has been inherited, that something is an enhanced ability to produce certain substances which destroy specific strains of bacteria and neutralize their toxins. The antibodies themselves have not been handed on from generation to generation, as is the case, for instance, in the transitory passive immunity found in the new-born young of an immune mother among mammals. But the capacity to produce the antibodies has been transmitted.

Moreover, we have no evidence to suggest that the antibodies conferring immunity against a specific strain of

bacteria are produced until the appropriate stimulus is applied, the stimulus being injection with bacteria of that strain. For example, acquired immunity in man against such diseases as measles or whooping-cough or diphtheria does not produce immunity in the offspring. The capacity to produce immunity is transmitted, but is not exerted until injection with the bacteria occurs. The immunity is not produced without the application of the proper stimulus. We can therefore qualify our conclusion and say that what appears to be inherited is an enhanced ability to produce certain substances when the appropriate stimulus is applied.

If we consider some known facts about immunity in human beings, we are at once struck by the fact that acquired immunity is generally only temporary even in the lifetime of the individual. An attack of some diseases—measles, whooping-cough, mumps, smallpox, chicken-pox, etc.—does confer an immunity that, in the vast majority of cases at least, appears to last for the lifetime of the individual, but in other diseases the immunity only lasts for a few years or even months. It hardly seems reasonable to expect that an acquired character that is generally only temporary in the lifetime of the individual in which it originated should be passed on to the following generations.

But although the immunity acquired by an individual in consequence of an attack by a given disease is generally only a temporary phenomenon and gradually disappears with the passage of time, yet we do find that a second attack of the same disease differs very considerably from the first. In some cases it is more, in others less severe. In the former class of case the severity of the second attack is probably due to the first having occasioned definite structural damage which leaves the organism more exposed to a second attack. In the second class, which probably includes the majority of bacterial infections, the mildness of the second attack can only be due to the first having left some permanent mark on the organism which

facilitates its reaction to the subsequent infection. The actual immunity conferred by the first attack may have passed away, but the stimulus of the attack has attuned the organism in such a way that it can react more promptly to the second attack. We have reason to think that each time a response to a stimulus is repeated by an organism the reaction of the latter is quicker and more marked. Each response to the stimulus attunes the organism for future stimulation. Topley and Wilson (1929) state:

It would appear that even long after all demonstrable antibodies have disappeared from the body fluids the tissues are left in a state of altered reactivity, so that they respond more briskly to any subsequent stimulus provided by the particular antigen in question. There is little doubt that the larger the doses of vaccine we give and the more often we repeat them, the more lasting will be the resultant immunity.

Vaccination, for instance, is infection with an attenuated strain of smallpox virus, and while we know that a first vaccination confers an immunity lasting about five years, we know that a second one confers an immunity lasting a much longer time, probably for life (Adami, 1918). Topley and Wilson (1929) quote Glenny and Sudmersen, showing that on a first injection of diphtheria bacteria into a horse there was a lag of about fourteen days, after which there was a slow and slight rise in the antitoxin content of the blood to a low maximum; it then sank again till the fifteenth week, when a second injection was given. "The response to this was of an altogether different character." Within four days a distinct rise of antitoxin was observable and the curve then rose steeply, reaching a maximum on the tenth day, and then declining fairly rapidly.

We see therefore that, though the stimulus has given rise to an acquired character which is only temporary, yet the response attunes the organism to the stimulus in a way that is much more permanent and influences the action of the organism should the same stimulus be repeated. The influence it exerts appears generally to be of such a nature that the organism can make the same response with more ease each time the stimulus is repeated.

It may perhaps be worth remarking that practically all the diseases in which a single attack appears to confer a lifelong immunity are characterized by long incubation periods—that is, the virus does not become actively pathogenic until a considerable period has elapsed after its introduction into the host. It may be that in these cases the apparent persistence of the immunity is due to the long incubation period. The actual immunity conferred by the first attack may not persist, but the attunement of the organism does and enables the host to develop immunity with much greater speed if a second attack should materialize, with such speed in fact that the host acquires immunity before the second injection has time to produce any pathological features. The attunement conferred by responding to the previous attack shortens the time necessary for the production of immunity until it is less than the incubation period of the disease. We know, for instance, that rabies has a very long incubation period, and if a man is infected with rabies we can start to produce immunity to the disease by suitable injections some time after he has been infected and yet be able to forestall the appearance of any of the characteristic symptoms of the disease.

It would appear therefore that in those cases where clinical immunity endures for some time, the antibodies themselves do not always persist. Topley and Wilson (1929), for instance, state:

A host of experimental and clinical observations make it certain that a man or animal may retain an effective degree of immunity after a natural attack of a disease, or after artificial immunization, long after the concentration of antibodies in the serum has sunk below the level at which their presence can be detected.

And most probably the cells of the reticulo-endothelial system and the lymphocytes are themselves replaced to a large extent in process of time. The problem of how an acquired immunity can be inherited by the following generations therefore only differs in degree from the problem of how an immunity acquired by an individual in early life

can be "inherited" by the same individual many years later. The antibodies have passed away, the cells which produced the antibodies have to a considerable extent been replaced, and yet the individual responds to a second attack more promptly and efficiently than he did to the first. I think that here we must admit there has been a transmission of the attunement to a stimulus at least to the daughter cells of the original reticulo-endothelial tissue and lymphocytes. Admittedly the cells of the body divide into daughter cells probably in all points equipotential to the parent cells, and this makes it easier to understand how the transference of an acquired character can occur in such cases, but still the two problems appear to be closely analogous.

We see then that we have some evidence that suggests that, when a strain of bacteria invades a host, the resultant immunity of the host, or at least the presence of the immunity-conferring substances, is only temporary, but the stimulus of the invasion has left the tissues of the host attuned in such a manner that, if bacteria of the same strain should invade him again, he can react to them with greater speed and efficiency. But the second series of experiments quoted above shows that in many cases, if the second attack should fall on the following generation, the increased speed and efficiency of the response is still shown, for the mortality rate in this generation is much lower than in the previous one and therefore the mean resistance is higher. This suggests very strongly that the attunement of the organism to the stimulus due to the first attack by the bacteria does not only persist for some time in the individuals exposed to that attack but can actually be transmitted, in some degree, to the following generation. This suggestion, if correct, explains many facts in the history of human diseases.

In some cases, *e.g.*, diphtheria in man, we find a high infant mortality rate, although most adults are immune, even though they have never had an attack of the disease. This probably indicates that, owing to the individual's

attunement to the stimulus, due to ancestral reactions to the disease, immunity can be produced in each generation by minute and sub-pathogenic doses of the bacteria repeated over a considerable time. If a child receives a pathogenic dose of the bacteria therefore he gets a bad attack and will probably die. On the other hand, the violent stimulation afforded by a regular attack of the disease may stir him up to produce full immunity. But if a child escapes a regular attack of the disease, the sub-pathogenic doses of the bacteria slowly stimulate him to produce immunity, and every year his chances of contracting the disease diminish, or at least the violence of the attack is lessened.

Again, in malaria-infected districts in West Africa we find that the natives have a high degree of immunity to the disease, but Europeans coming to the districts, fresh from parts of Europe where malaria is not found, have no immunity at all. Further, among the natives the immunity, even after some thousands of years of exposure to the disease, does not arise until the individual is some years old, and the disease still causes a high infant mortality rate. The awakening of immunity still requires stimulation for some time by the environment. Some years ago Negro troops were occasionally sent from the West Indies to West Africa. They were descendants of slaves imported from West Africa into the West Indies. On arrival in West Africa they suffered severely from malaria during the first season, but thereafter were immune. The white officers, however, continued to suffer. The Negro troops' attunement to the stimulus of an attack of malaria, derived from their ancestors' response to the disease, though weakened by the residence of a few generations in the West Indies, enabled them to make a prompt and enduring response to the infection. But the white officers, whose ancestors had not been inoculated with the disease and who were therefore not attuned to the stimulus, made only a weak and transitory response (Reid, 1905).

We also have reason to think that northern Europeans have developed a very considerable degree of immunity to tuberculosis. But among the natives of the South Sea Islands, whose ancestors had never been exposed to the disease, tuberculosis has caused frightful ravages (Hirsch, 1881). Measles also among the natives of these islands was a dreadful malady, but among Europeans, descended from ancestors long exposed to the disease, it has become a comparatively mild complaint of childhood.

We have therefore evidence that suggests very strongly that invasion by bacteria produces a reaction in an organism that is only of a temporary nature, but the reaction leaves the organism attuned to that particular stimulus in such a way that it responds more promptly and fully if the same strain of bacteria should repeat the invasion, and that this attunement to the stimulus appears to be transmitted in some degree to the next generation, for the accelerated response also occurs in them if the appropriate stimulus is applied. Something has therefore been inherited. But we have considerable evidence that this something is only inherited temporarily, and that, if the race is kept in a new environment in which the effective stimulus is lacking, the inherited character will slowly disappear. In the first series of experiments given above we saw the tendency for resistance to a given strain of bacteria to diminish in successive generations if the race was kept in an environment free from the effective stimulus. In such an environment, therefore, selection for susceptibility increased susceptibility, but selection for resistance did not lead to any increase of resistance; in fact, resistance appeared to diminish slowly in the contrary direction in spite of selection, except in one experiment where a very slight and rather doubtful increase was alleged. Besides, if this type of inheritance was not of a temporary nature, every species would soon acquire a complete immunity to any pathogenic organism to which it was exposed. We must remember above all that no visible character has been inherited; it is an attunement to a given

stimulus that has been transmitted, and if this stimulus is absent from the environment the attunement to it can not manifest itself.

Moreover, the inherited attunement is something quite different from the inductions mentioned by Conklin, for it is inherited for several generations albeit in a progressively decreasing degree. In Webster's second experiment quoted above, the first generation of the resistant line displayed a considerable attunement to the stimulation of invasion by the same strain of bacteria as had been injected into its parents. The mortality rate was therefore considerably lower than in the parents' generation, and this lowered mortality rate was inherited over several successive generations, although it did tend to fade out somewhat in the later ones. Lambert and other experimenters also crossed the races of high resistance with those of low, and though the results were doubtful they did not give any evidence of inheritance according to Mendel's laws. It is on these grounds that I have postulated the existence of a type of temporary inheritance, but further evidence of its temporary nature will be offered later.

If the above is true, then an acquired character is—in these experiments at least—not directly inherited, but an attunement to a given stimulus appears to be inherited temporarily for some generations and then, if the effective stimulus remains absent from the environment, slowly disappears. The character therefore has not become an inherited one in the sense of the geneticists; it does not develop independently of the environment, it is not permanently inherited but dies out in the course of a few generations if the effective stimulus is absent from the environment, and it is very doubtful if it obeys Mendelian laws of segregation. But something appears to have been transmitted from parent to offspring that endures for some generations, and as this something can be transmitted by either parent it presumably is conveyed in the germ cells and therefore is inherited in the ordinary sense of the term. We appear to have no evidence as to which exact part of the germ cell acts as the vehicle of this inheritance.

Have we, however, any reasons for thinking that adaptive acquired variations, other than resistance to invasion by a given strain of bacteria, are subject to similar laws and can be inherited temporarily? Before considering this question it may be well to recapitulate the outline of the theory here advanced. Many, if not all, species if placed in a new environment acquire individual adaptations which fit them for their new surroundings, and those acquired characters are never exactly identical in all individuals but vary over a certain range. If we select those individuals in which the acquired character is best developed and breed from them, we will get a generation of offspring in which the character will develop to a slightly higher average than in the preceding generation. This is due to the fact that we really are selecting those individuals in the first generation which are most responsive to the new environment and breeding from them. As a result we will obtain a second generation with a higher average responsiveness and therefore they will acquire the character to a slightly higher degree. There is no evidence here of the inheritance of anything but a certain degree of responsiveness to the environment. The results of the second series of experiments given above could be easily explained in this way, were it not for the fact that the first series demonstrated clearly that selection of the most responsive individuals in each generation and breeding from them did not lead to any marked progressive increase of resistance. Selection alone therefore can not explain these facts. But if we exclude or minimize the influence of selection by breeding from all the members of the first generation subjected to the new environment and find that in the second generation the acquired adaptive characters are developed to a higher degree than they were in the first one, and that in further generations there is a still further progressive increase in the adaptation, we have definite evidence that something has been transmitted. The second generation responds to the new environment more readily than the first one did. The

acquired character itself has not been transmitted, but the attunement to the stimulus of the new environment consequent to the first generations' response to that stimulus has been transmitted and therefore the second generation responds more readily to the same stimulus. For if the acquired character left no mark whatever that could be transmitted to the next generation, then each generation should acquire the character to the same average degree, subject of course to variations in the intensity of the environmental stimulus, which possibly fluctuates slightly both upwards and downwards. We also must ensure that a process of natural selection does not occur. Those experiments therefore are most suitable in which the great majority of the individuals subjected to the new environment both survive and reproduce. Further, it must be remembered that experiments of this nature have rarely been tried. Most workers have looked for the direct and immediate inheritance of an acquired character completely fixed and independent of the environment. This rarely, if ever, occurs. Such observations as we have in support of the theory here advanced have been made almost by accident in the course of investigations made for other ends. Moreover, as the possibility of any inheritance of an acquired character is generally denied, we must exclude any experiments or observations that admit of any other explanation, however far-fetched and extravagant such explanation may appear to be. These considerations necessarily limit our available evidence. Of course, as already stated, this paper does not contend that acquired adaptations are inherited in the geneticists' sense of the term, but it suggests the existence of another form of heredity.

To begin with plants, Vernon (1903) quotes Lesage, who cultivated various plants under similar conditions, except that some of them were watered with water containing common salt, and he found that characters were developed similar to those exhibited by maritime plants. He in this way succeeded in altering the common garden cress,

Lepidium sativum, in which the palissade tissue became more developed and possessed an extra layer; the lacunae became less pronounced, and the chlorophyll less abundant. On sowing the seeds of this plant a second year and again treating the plants with salt water, a still more marked result was obtained. Vernon comments on this case, "it appearing," he remarks, "as if the alteration in the tissues of the second generation was carried on more or less from the point gained in the first."

Henslow (1908) experimented with the common rest-harrow, *Ononis spinosa*. He obtained specimens growing in a very dry situation and possessing well-developed spines, and seeds obtained from these were grown in a very moist atmosphere and soil. They all grew well, but in the first generation the spines were very much reduced. Seeds were collected from these plants and again grown in the moist environment. In the second generation the plants flourished and all of them blossomed, but the spines were completely absent. The plants of the second generation presented no appreciable difference from *O. repens*.

De Vries (1894) carried out some experiments with crow-foot, *Ranunculus bulbosus*. During the years 1886 and 1887 he counted the number of petals in large samples of this flower collected near Hilversum. The great majority had five petals, a few had more, and none had less than this number. The actual percentages of flowers with five petals in each year were: 1886, 92.6 per cent.; 1887, 90.8 per cent. In the spring of 1887 some of these plants were transplanted into De Vries' garden, where apparently they met with much richer soil than they had been used to. All the plants grew, and in 1888 a sample yielded only 59.9 per cent. of flowers with five petals, all the remainder of the flowers having a higher number, mostly six or seven. None had more than ten. De Vries discarded the flowers having five petals and collected seed from the remainder. He sowed this seed during the next two years but appears to have made no counts. In the fourth year he raised another generation, presumably from seed obtained from

the plants sown in 1890, but does not state if any selection was practised when collecting the seed. No counts apparently were made on the 1890 plants, so presumably no selection was carried out. In 1891 a count was made, and only 35.5 per cent. of the flowers had five petals, all the remainder had more than five, and two had twelve and thirteen, respectively. The amount of selection practised on this line was almost negligible, and it would appear that the influence of the richer soil which affected the first generation on their removal into the garden acted with even more force on the following generations. But the case is not entirely satisfactory, for a very slight amount of selection was carried out.

Bordage (1910) carried out extensive researches on the European fruit trees introduced into the island of Reunion. He noticed that peach trees which had been a long time in the country had become almost evergreen. He therefore introduced peach stones from Europe, where the peach tree sheds its leaves every winter, and raised them in Reunion. The peach stones were sown in 1895. The trees raised from them shed their leaves completely, but the time of complete bareness was reduced to approximately one and a half months. In the following years the period of complete bareness was gradually reduced and by 1905 the trees had become "sub-persistent" in their foliage—the young leaves appearing before the old leaves were shed. The environment had stimulated the trees and each year the stimulus had produced its effect more easily than the year before, and the growth of new leaves took place a little earlier, till finally it overlapped the shedding of the old leaves. Bordage then obtained seeds from these peach trees and raised them in Reunion. The resulting trees were almost sub-persistent from the beginning; the new leaves appeared before the old ones had all fallen. The stimulus in the environment obviously produced an effect much more quickly in this generation than in the one before. It should, however, be stated that Bordage had left Reunion before the second generation

trees had grown, and he had to rely on the observation of others in regard to the behavior of these trees.

Shull (1926), apparently with such cases in mind, remarks: "In most or all of these cases, the effect of the environment is purely temporary, though in some instances the modification may persist in gradually diminishing degree for several generations. It has nothing to do with heredity." With all respect to Shull, if the modification persists in any degree for several generations, it quite obviously has a great deal to do with heredity, though not perhaps with heredity in the narrow sense in which geneticists use the term.

Walker (1936) quotes von Nageli, who transplanted Alpine plants into the botanical gardens at Munich. In a few years they completely altered their characters and lost the typical features of a mountain flora. Seed obtained from these plants, when grown in Munich, produced plants with the new characters of their parents. I have not been able to obtain von Nageli's paper, but apparently the original plants took some time to lose their mountain characteristics, while their offspring lost them much more rapidly. The new environment seems to have acted more rapidly on the offspring. Seeds of these again planted in the mountains of course produced the typical mountain features, but I can not say if there was any noticeable delay in their doing so. This experiment at least shows that the features of an Alpine flora are not inherited in the geneticists' sense of the term, for when the environment was altered they disappeared.

Darwin (1868) gives a case of American maize becoming acclimatized to Europe, but de Vries (1909) objected that this transformation was in reality due to hybridization, and his objection seems to exclude the case.

Countless observations (see especially Maximov, 1929) have been made to the effect that lowland plants removed into the Alps develop features similar to those which characterize Alpine plants, and countless experiments of the opposite kind show that Alpine plants moved to the

lowlands acquire the features of lowland plants. In both cases there is some delay in the change of features. This at least shows that the characteristic features of both lowland and highland plants are only temporarily inherited and are not independent of the environment. Succulent maritime plants also tend to lose their succulence if transplanted inland, and we have already seen that some inland plants develop succulence if watered with salt water. These characteristic features of local flora are generally regarded as inherited, but in the light of these facts we can see that the inheritance is only temporary and they tend to die out in the course of a few generations if the stimuli that gave rise to them are absent.

Ferrera (1899) points out that barley grown for a few generations in different latitudes becomes adapted to the different lengths of the summer. In northern latitudes it grows and ripens more quickly possibly on account of the longer days. Thus from the time of sowing to complete ripening in southern Norway is about 117 days, but in the north of Norway it is only about 76 days or less. Seeds from barley plants which have been grown for a few generations in northern Norway, when sown in southern Norway retain for three or four generations their habits of rapid growth and early ripening. Possibly a certain amount of natural selection acted on the plants when they were first sown in the north, and only early ripening ones were able to propagate themselves. This would result in the production of an early strain. But if natural selection alone had produced the early strain the characteristics of the race should have been retained indefinitely or only have faded out very slowly after the race was moved to a more southern climate. But when the seeds of these plants are sown in more southern and favorable climates, the early characteristics do not persist indefinitely but fade after a few generations. Natural selection could not effect this fading of a characteristic that is not a handicap in the southern climate, though absence of selection for earliness might lead to its disappearance in the course of

many generations. De Candolle (1875) obtained very similar results on transplanting trees from cold to warmer climates.

Turning next to the fungi, Vernon (1903) quotes Ray as sowing conidia of the mould *Sterigmatocystis alba* in solutions of glucose. At first growth occurred very slowly, but in successive generations it became more and more rapid, until in the sixth generation the growth was more advanced at the end of eight days than it had been in the first generation at the end of fifteen. The morphological characters of the fungus were also progressively changed until it came to resemble *penicillium*.

Ferrera (1899) quotes Hunger, who experimented with *Sterigmatocystis nigra*. He grew one culture in pure Raulin solution, another for one generation in Raulin solution plus 6 per cent. NaCl, and another for two generations in the same solution. All cultures were maintained at a standard temperature, and exactly the same amount of fluid was used in each experiment. The conidia from these three cultures were designated A, B and C, respectively. He then sowed the conidia from A, B and C in the three following solutions: Normal salt-free Raulin's solution, Raulin's solution plus 6 per cent. NaCl, and Raulin's solution plus 18.4 per cent. NaCl. The results obtained were as follows:

I. Normal salt-free Raulin's solution	Germination:
A	In 4 days
B	" 5 "
C	" 5 " (less prolific than the others)
II. Raulin's solution plus 6 per cent. NaCl	Germination:
A	In 5 days
B	" 4 "
C	" 3½ "
III. Raulin's solution plus 18.4 per cent. NaCl	Germination at end of 5 days:
A	None.
B	Very slight. Visible under microscope.
C	Distinct. Visible to naked eye.

Conidia were then collected from the first experiment tabulated above, *i.e.*, from A, B and C grown for a generation in normal salt-free Raulin's solution. These were called A 1, B 1 and C 1, respectively, and were sown in Raulin's solution plus 18.4 per cent. NaCl. The following results were obtained:

		Germination after 5 days:
A 1	None.
B 1	Very feeble and rare.
C 1	Feeble but visible to naked eye.

Here the attunement of the C 1 conidia to a solution of NaCl through their great-grandparents' and grandparents' having lived in such a solution persisted in some degree, even though their immediate parents had lived in a normal salt-free solution.

As regards animal life, and beginning with the lower forms, we have several experiments with insects. Durken (1923) experimented with the common white butterfly, *Pieris brassicae*. The pupae of this butterfly are usually a dirty-white color with black specks, but if the caterpillars are treated with colored light during the pre-pupal stage, the color of the pupae is altered. Red or orange-colored light causes the pupae to be almost free of pigment, in which case the green color of the underlying tissues shines through their skins and they appear green. Durken treated some of the pupae with red light and others with orange-colored light. He found that in normal wild pupae 3.72 per cent. were green, but in his treated pupae, taking those treated with red and orange light together, there were 69.11 per cent. green. The offspring of these green pupae were divided into three lots; one was allowed to develop in normal light, one in darkness and the third was again treated with orange light. The percentages of green pupae were as follows:

Treated in orange light	94.89 per cent.
Rearred in normal light	48.48 " "
Rearred in darkness	41.00 " "

The experiment was repeated, but the influence of the colored light was restricted to the immediately pre-pupal stage. The following percentages of green pupae were obtained:

Original wild butterflies	3.72	per cent.
First generation treated	62.89	" "
Second generation treated	98.24	" "
Second generation reared in normal light	48.52	" "
Second generation reared in darkness	43.27	" "

On account of the fact that the percentage of green pupae in the second generation was markedly higher than that found in the wild butterflies, even though these second generation pupae were reared in darkness or normal light, Durken declared that the acquired green coloration of the pupae was inherited. This indeed appears to be the case, but it is exceedingly doubtful if the character was inherited permanently, and in all probability it would die out in the course of a few generations. But it is evident that the reaction of the second generation to the stimulus was more marked than the reaction of the first. It seems highly probable that what was temporarily inherited in this case was an attunement to a stimulus. This is rather confirmed by some further experiments of Durken. He selected some heavily pigmented pupae and treated them in after life with orange-colored light. No change, of course, was produced in them, but when their offspring were treated with similar light these yielded no less than 96.01 per cent. of green pupae, but similar offspring reared in normal light or darkness varied very little from their free ancestors. Durken assumed that orange-colored light produced no effect if applied after the pigmentation of the pupae had occurred, because the offspring of such pupae displayed no marked increase of green pupae when reared in darkness or normal light, and he accounted for the very high percentage of green pupae in such offspring when treated with orange light as being due to the direct effect of the light on that immediate generation. But the percentage of green pupae in these off-

spring when treated with orange light is altogether exceptional if it was due merely to the direct effect of the light on them. It seems more reasonable to conclude that the treatment of the adult parents had attuned them to the stimulus of orange light, though it produced no visible effect in them, and that this attunement was transmitted to the next generation. In a repetition of this experiment all the non-green pupae in a given line were selected and when adult were treated with colored light; their offspring, when treated with orange light, yielded actually 99.20 per cent. green pupae. These last experiments on the offspring of non-green pupae are very useful, for they prove that the results of Durken's experiments on the offspring of green pupae were not due in any way to selection. Simultaneously with Durken, Brecher (1923) obtained very similar results working with *Pieris brassicae* and *Vanessa Jo*.

Harrison (1928) repeated these experiments with very similar results. He took specimens of *Pieris napi*, six females, which yielded 255 eggs. These were divided into three lots; one was treated with normal light, one with orange light and one with blue light. The following were the percentages of green pupae obtained:

Treated with normal light	20.9 per cent.
Treated with orange light	93.4 " "
Treated with blue light	21.9 " "

Green pupae from the orange-treated lot were selected and allowed to breed in large cages under conditions as nearly natural as possible. Their offspring were again treated with orange light, and the process was repeated for the following generation. The following percentages of green pupae were obtained:

Second generation	95.2 per cent.
Third generation	100.0 " "

One more generation was reared and was placed in variously-colored surroundings. They yielded 58 per cent. green pupae.

Metalnikov (1924) carried out researches on the caterpillars of *Galleria mellonella*. By rearing them at an optimum temperature he could obtain several generations in the one year. The caterpillars are highly susceptible to invasion by the cholera vibrione. Metalnikov injected minute doses of a cholera vaccine into the young caterpillars, the dose being repeated two or three times. They were then reared and bred from. Half their offspring were again vaccinated and used to perpetuate the line; the other half were given a normally fatal dose of the cholera vibrione. The percentage of survivors in the half of each generation tested was calculated and the following results were obtained.

	Percentage surviving
1st	0
2nd	0
3rd	30
4th	16
5th	0
6th	42
7th	45
8th	72
9th	75

Inoculation with the vaccine would stimulate the caterpillars to produce an active immunity against the disease, and this active immunity was probably only temporary. But apparently the response of the caterpillars to the vaccine left them attuned to the stimulus of invasion by the cholera vibrione, and this attunement was transmitted and progressively increased in each generation by repetitions of the inoculation, until finally the caterpillars of the ninth generation were able to respond so promptly to an invasion by living and virulent bacteria that 75 per cent. of them survived. The falling off in the resistance of the fourth and fifth generations was attributed by Metalnikov to the fact that he had used enormous doses of the vaccine in injecting the second and third generations. The large doses were apparently less effective than the small ones in producing immunity, and in the fifth generation small doses were again used.

Harrison (1927) experimented with *Pontania salicis*, a sawfly, which normally lays its eggs on several species of willow but each race apparently keeping more or less fixedly to the same species. He selected individuals which laid their eggs in *Salicis Andersonia*. These were reared in a locality where *S. Andersonia* was absent but *S. Rubra* was present. Many flies laid in *S. Rubra*, but many of the galls aborted. A year later more sawflies were added to the colony, and two years later it seemed well established. The next year some trees of *S. Andersonia* were planted in the locality. Two years later, although the colony of sawflies was well established, no galls were found on *S. Andersonia* but abundant galls on *S. Rubra*. Walker (1936) explained this case as one due to selection. There may have been an element of selection operating once the experiment was started, but selection can not induce an insect to lay eggs on trees on which it does not normally lay. But possibly such species are more elastic in their choice of a breeding-place than we are apt to think, and instances have occurred in nature of species changing their selection of a living place from unknown causes. Carpenter (1921), for example, cites a case of a capsia bug which was wont to feed on willows suddenly changing its habits in several localities and taking to feeding on apple trees.

Dealing with animals living in a different sphere, we have Schmankewitsch's famous observation of the conversion of *Artemia salina* into *A. milhausenii* (quoted from Bateson, 1894). The point of this observation is that by a gradual concentration of the salinity of the water one form of *Artemia* was changed in the course of a few generations into another form. Bateson rightly makes the point that these two forms should not be regarded as distinct species. It appears to be admitted that sudden transplantation of one form into water with a considerably higher salinity than that to which it was accustomed would most probably lead to its immediate death. Bate-

son himself admits this for such forms as Copepoda and Cladocera. However, if the salinity is slowly increased, the individuals become acclimatized to it. But as several generations elapsed during the process of acclimatization, this means that each generation hands on its stage of acclimatization to the next, or the successive generations become attuned to the stimulus of increased salinity and are able to respond more markedly and rapidly. However, no permanent change has been effected. If the stimulus is removed, the race will slowly revert to its former state. Schmankewitsch repeated the above conversion experimentally and claimed that by breeding *A. salina* in progressively diluted water he produced a form similar to *Branchipus*.

Bateson (1889) himself recorded rather comparable facts. On the north shore of the Aral Sea three shallow basins were left by the drying-up of the sea, and in time these basins also shrank, becoming more and more salty. In the process they left seven terraces and Bateson collected specimens of the shells of *Cardium edule* from each of these. As the shells were traced from the highest and oldest terrace down to the lowest and newest, they were found to have undergone progressive changes as follows: the shells became thinner, the beak smaller, the shells more highly colored and their length increased in relation to their breadth, the ridges between the grooves appeared on the inside of the shell and, in the lowest terrace especially, the absolute size of the shells was much reduced. As these changes were so universal and uniform Bateson concluded they must have arisen owing to the action of the environment, for exactly similar changes were found to have occurred in a salt lake in Egypt, although the ancestors of the cockles found in the Egyptian lake presumably came from the saline Mediterranean, while the ancestors of those found in the Aral Sea basins must have lived for generations in the brackish Aral Sea. He made a possible exception in the changes in the length-breadth ratio of the

shells, for this change was not so uniform. But he records that in the Aral Sea basins the change was "far more marked in shells of greater absolute size (that is, presumably, of greater age) than in smaller and younger ones." This must mean that the character was to some extent acquired by each generation, and appears to have been acquired to a greater degree by the later generations. Successive generations had apparently been more and more attuned to some stimulus in the environment which evoked this peculiarity of growth.

Kammerer (1924) dealt with animals rather higher in the evolutionary scale. A slight cloud overhangs his results, but he appears to have been a careful and conscientious worker and, whatever mishap led to his unfortunate death, nobody has ventured to repeat his experiments and contradict his results. His experiments with the midwife toad (*Alytes obstetricans*) furnish another example of an acquired adaptation becoming progressively more marked in successive generations. Most frogs and toads lay their eggs in water. The eggs are small with little yolk and are surrounded with gelatinous capsules which swell up when they come in contact with the water. The tadpoles on emerging from the egg have no specialized respiratory apparatus, but shortly after hatching they develop external gills. These are soon lost and internal gills take their place. Later the tadpoles lose their tails and develop limbs.

The midwife toad, however, deposits her eggs on land. These eggs are large and are carried about by the male, adhering to his hind legs, until the young are hatched. The latter on emerging from the egg have passed the stage of external gills and already possess internal gills. They as yet have no limbs but later on, like other tadpoles, they develop these and lose their tails.

Kammerer first subjected the eggs to heat and comparative aridity. Small tadpoles resulted which had already developed limbs at the time they were hatched. These

tadpoles in turn produced large eggs with much yolk and fewer in number, and in Kammerer's words "from generation to generation produce eggs that are proportionately more limited in number, but are larger and longer and more and more rich of yolk." If the environment was kept warm, comparatively dry and shady, tadpoles hatched from the later eggs with fully developed limbs. On returning the eggs to water, there was at once a tendency to revert to the usual state of development for the hatching tadpoles. Here again we see a progressive increase in the efficiency of the response to an altered environment in successive generations.

Kammerer then reversed the experiment and forced the midwife toad to breed in water. Here a remarkable change occurred in the few eggs which survived. They produced tadpoles, with a single pair of external gills, which later became large toads. The eggs from these had little yolk and in further generations the yolk became progressively decreased until it disappeared. Further, the gills became increased progressively until in the fifth generation there were three pairs of external gills. And more remarkable still, the males in these water-living toads developed the nuptial pads on their fingers and forearms which are not present in the land-living midwife toad. These changes are of an atavistic nature, but they prove conclusively that features always present in the midwife toad in nature and generally regarded as inherited are in fact only responses to an external stimulus. But the organism has become so attuned to the stimulus by countless generations of its ancestors being exposed to it, that its response is immediate. If, however, the appropriate stimulus is diminished, the response also slowly disappears. It should be pointed out that some authorities who saw Kammerer's specimens doubted if the structures he had described as nuptial pads in the midwife toad were really of this nature.

Kammerer (1924) tried rather different experiments with the spotted salamander (*Salamanandra maculosa*),

which normally bears about fifty young at a time. The latter are larvae living in the water and possessing gills and a finned tail. Later they develop lungs and limbs and lose their tail fins. Kammerer kept the mother salamander out of water and compelled her to produce her young on dry ground. The larvae when born had to be placed at once in water or they would have perished. The process was repeated in the next pregnancy. In this case the larvae when born were longer and more developed. In the fourth pregnancy the young were born with fully developed lungs and limbs and a finless tail. But the number of young produced at a birth was reduced to six or less, the remainder of the eggs liquefying and serving as nourishment for the surviving larvae. This experiment does not of course deal directly with heredity, but it furnishes a very good example of a response being progressively increased each time a stimulus is repeated, and the organism becomes attuned to the stimulus.

Kammerer's experiments in color changes* in the spotted salamander also show this progressive increase of a response in successive generations. The normal wild spotted salamander in the neighborhood of Vienna is black with yellow spots. Kammerer discovered that specimens kept against a black background gradually turned blacker, but specimens kept against a yellow background gradually turned yellower. What should we find in their offspring? If their parents' response to the color of the background produced an attunement to the stimulus afforded by that particular color and if this attunement was transmitted to them, we should find that the offspring of the black background parents react to a black background more quickly than normal wild salamanders do, but they should react to a yellow background more slowly than do wild salamanders, for their immediate parents made no response to a yellow environment. This is exactly what we do find. The offspring of the black background parents, if kept against a similar background, are

blacker at the end of two years than their parents were at the end of four, but if kept against a yellow background, they are slightly less yellow at the end of two years than normal wild salamanders kept for a similar time against the same background. The attunement to the stimulus resulting from their parents' response has been transmitted to them and enables them to make the same response to the same stimulus with greater ease, and the absence of any response to yellow in the parents' lifetime hinders the offspring in responding to that color. The offspring of the yellow background parents gave equally strong evidence in support of the belief that the attunement of the parents' response is transmitted to the following generations.

It should perhaps be emphasized here that Kammerer was not looking for such results as these and in fact did not notice them. He was searching for evidence in support of the idea that acquired characters are directly inherited. This therefore excludes the possibility of any of these experiments being in any way tampered with to produce these results. It is not a case of "the eye seeing what the eye looks for." The results were recorded by Kammerer without any realization on his part of their significance. The same may be said of nearly all the experiments mentioned in this paper. None of the experimenters realized or noticed the fact of the increased response in each successive generation to the same stimulus. They were all looking for the direct inheritance of an acquired character. And Kammerer's results can not have been due for the main part to the direct inheritance of an acquired character, for the offspring of his black-background and yellow-background salamanders were at first only very slightly, if at all, more black or yellow, respectively, than their parents had been at the commencement of the experiment. At least in Kammerer's colored pictures they are not shown as noticeably more black or yellow.

Kammerer (1924) records another experiment which is even more convincing. He took specimens of a lizard (*Lacerta serpa*), which normally has a green back with three brown longitudinal stripes, and kept them at a temperature about 15° F. above that which they usually lived in. In 18 to 24 months the lizards had become perfectly black. He then placed the blackened lizards in their normal temperatures and allowed them to lay their eggs. From these eggs, he states, "almost normally colored young emerged." Later these young were kept at a temperature intermediate between their normal and the very high one in which their parents had been placed, and they all turned black. Kammerer thought the experiment was a failure when the normal young were born, and from his point of view it was, for it proved that the acquired character was not directly inherited. But the point is that a considerably slighter stimulation than had been applied to their parents produced the same response in the offspring and apparently in a shorter time.

We have to keep in mind that every individual begins life as a single cell, and we do not inherit our arms and legs from our ancestors, but we do inherit a capacity to grow limbs very similar to the ones they possessed. What we inherit therefore is a capacity for a certain type or pattern of growth. But we can not expect that something from outside impressed on the organism can be inherited, for it has not altered the growth capacities of the germ cells in any way. Mutilations therefore are probably not inherited, but the attunement of an organism to the stimulus supplied by a mutilation might be inherited. This is well shown in Kammerer's (1924) experiment with the Ascidian *Chiona intestinalis*. He cut off the siphons repeatedly, and each amputation was followed by the regrowth of the organs, which however grew a little longer each time the operation was repeated. The offspring of these individuals were found to have rather longer siphons than normal ascidians. The mutilation was not inherited, but the response to the mutilation, *i.e.*, increased growth of

the siphons, did appear in the following generation. In a normal ascidian there must be a stimulus to produce growth of the siphons, and the continuous exercise of the response by Kammerer's removing the siphons attuned the organism more delicately to this stimulus, and this attunement was apparently transmitted to the next generation and produced excessive growth of the siphons.

With regard to birds, Darwin (1868) mentions the case of the domestication of the wild duck, as follows:

An accurate and well-known observer in England has described in detail his often repeated and successful experiments in domesticating the wild duck. . . . His young birds always changed and deteriorated in character in the course of two or three generations; notwithstanding that great care was taken to prevent any crossing with tame ducks. After the third generation his birds lost the elegant carriage of the wild species, and began to acquire the gait of the common duck. They increased in size in each generation, and their legs became less fine. The white collar round the neck of the mallard became broader and less regular and some of the longer primary wing-feathers became more or less white. . . . His birds continued to pair together and never became polygamous like the common domestic duck. I have given these details because no other case, as far as I know, has been so carefully recorded by a competent observer of the progress of change in wild birds reared for several generations in a domestic condition.

The progressive nature of these changes is apparent. It should be stated, however, that earlier in the same work Darwin records that Tibertius in Sweden claimed to have raised wild ducks for three generations, but though they were treated like common ducks, they did not vary even in a single feather. Darwin himself does not appear to have credited Tibertius' claim.

De Quatrefages (1883) refers to the case of the Egyptian goose (*Anser egyptiacus*), which was introduced into France in 1801 by Geoffrey Saint-Hilaire. At first it continued to lay in December, a very awkward time, but in spite of this many generations were raised. The time of egg-laying became later, and in 1844 the birds were laying in February, and in 1846 in April, the same time as the ordinary domestic goose.

Apart from the experiments on the inheritance of immunity given at the beginning of this paper, there are

unfortunately few experiments or observations on mammals which throw light on this subject. Darwin (1859) in the "Origin of Species" remarks in three separate places that, if a peculiarity arises in an individual, it usually appears in its offspring at the same period of life as that in which it appeared in the parent *or a little earlier*. He points out that in some cases it could not be otherwise, as, for instance, if peculiarities arise in the horns of cattle, they can not appear in the offspring until the latter have grown horns, but he observes that the rule has a much wider extension than can be explained by this fact, and that many peculiarities appear in the offspring at the same age as they appeared in the parents, though there is no known reason why they should appear at that particular time. In his "Variations of Animals and Plants under Domestication" (1868) he gives several instances of this fact. These are, for the most part, inherited diseases and ailments, *e.g.*, blindness, deafness and insanity and cases of excessive hairiness or peculiar growths. If these features first arose as a response to some unknown stimulus in the environment and the attunement of the organism to this stimulus was transmitted to the offspring, we can see that, if the stimulus continued to act, the second generation would acquire the character more easily and therefore a little sooner.

The case of the rabbits on the island of Porto Santo near Madeira is of great interest. These were introduced from Spain in the year 1418 or 1419. One female rabbit and her offspring actually were the ancestors of the entire stock, and as this rabbit came from Spain, where ordinary wild rabbits abound, we have no reason to think there was anything exceptional in her characteristics. In Darwin's time the island abounded with rabbits, but they were considerably smaller and lighter in weight than the common European wild rabbit, the upper surface of the body was reddish, the under parts were grey, and the ears and tail lacked any signs of black. All the rabbits on the island were of this coloration, and they were also shy and noc-

turnal to an unusual degree. Quite evidently the race had varied very considerably since its introduction into a new environment almost 400 years previously. If this variation was due to the arising of mutations, which in some way favored the preservation of the species and which would be preserved by natural selection, while the non-mutant individuals were destroyed, the variety should be permanent and should not be immediately affected by alteration of the environment. But Darwin records that four of these rabbits brought to England, though refusing to breed with English rabbits and retaining many of their peculiar habits yet, in less than four years, began to display some of the coloration typical of English wild rabbits. Their ears were edged, and the upper surface of their tails was covered with black or blackish hairs. The characters of the Porto Santo rabbits were not inherited, therefore, in the geneticists' sense of the term; they were not permanent, but if the stimulus of their peculiar environment was removed, they slowly disappeared. They were really responses of the individual to its environment, but owing to the long ancestral exposure to this environment the rabbits had become so attuned to the stimulus that their response was immediate and complete. But removal of the stimulus led to the slow fading of the response.

Lydekker (1903), writing on the acclimatization of the Indian spotted deer or chital in Europe, states that at first nearly all the fawns perished owing to having been born in winter. Subsequently the females took to calving in spring, after which breeding has gone on successfully. Although Lydekker does not state whether the change was gradual or not, it appears that this case was very similar to that of the introduction of the Egyptian goose into France, mentioned earlier in this paper.

In the same work Lydekker mentions that Barret-Hamilton introduced hares, which changed their coat-color in winter, into southern counties. For several seasons, al-

though they were now in an environment where snow rarely fell, hares were seen in winter in the white coat characteristic of northern districts, and then the white coats gradually disappeared. Here again we see that the coat-color in winter was merely a response to a particular environment and that when this environment was altered, the seasonal change of coat gradually ceased. A response to a particular stimulus was temporarily inherited and, when the stimulus diminished, the response faded and the attunement to the stimulus passed away. Unfortunately we can not say in this particular instance whether the hares in which the change of coat diminished and finally ceased altogether belonged to the generation that was actually transferred from the northern environment, or to their descendants. But the point is really immaterial. At first on their transfer to a southern climate their attunement to the stimulus of cold was so accurate that it produced the change in coat-color, although the actual strength of the stimulus was much below that to which they had been accustomed. But on moving south they were exposed to the new stimulus of a mild winter and their attunement to this gradually became more and more delicate and finally overcame the fading attunement to cold conditions. In their descendants certainly no seasonal change of coat occurred, which showed that the gradually acquired attunement to the stimulus of a mild winter was dominant in them.

The sea-otter of the Pacific coasts is also mentioned by Lydekker. This animal used to breed and rest on land and feed close inshore, but after the terrible persecution which it endured at the hands of whalers it gradually altered its habits, and now breeds and rests on large floating masses of seaweed, and feeds in thirty fathoms of water. Its racial experience has slowly attuned it to the stimulus of the presence of man.

As regards man himself, we have very few records and observations to assist us. Most authorities appear to agree that white men can not become acclimatized to the

tropics. Woodruff (1905, 1909), for instance, gives a great deal of evidence on this point. Ridley (1899) also appears to be of this view, or at least thinks that such an acclimatization can only occur when the racial movement towards the tropics is carried out very slowly. Huntington (1922) mentions the case of the United Empire Loyalists who moved to the Bahamas from Georgia and other southern states at the end of the American War of Independence. Since that time the stock has greatly degenerated in vigor, and he quotes one inhabitant as stating, "We are weaker than our fathers, and they were weaker than theirs." Yet these people, if moved to another climate, showed a marked improvement. People of the same stock moved at the same time into Canada, where their descendants constitute a vigorous and virile people. And the Bahamas are not infested with any serious disease. The hookworm is practically unknown and malaria no more prevalent than in Delaware. It appears that an attunement to a stimulus, in this case unfortunately producing a very unfavorable reaction, has been inherited and augmented in each generation.

I have avoided citing any instances taken from the bacteria or protozoa, as their methods of reproduction are rather exceptional, but perhaps brief mention might be made of Dallinger's (1887) experiments with the Flagellata. By gradually raising the temperature in which these lived over a period of almost six years, he acclimatized them to live in a temperature of 70° Centigrade.

In all the aforementioned cases we see the same phenomenon. Individuals exposed to a new environment acquire modifications, either structural or functional, which adapt them to it. Their offspring, if still subjected to the same environment, acquire the same adaptations but do so more quickly and to a more marked degree than their parents did. If each successive generation set out from the same starting-point and acquired the adaptation for itself, then each generation should acquire it to approximately the same degree. The fact that the successive

generations acquire it to a progressively higher degree shows that some influence arising from one generation's response to the environment is transmitted to the following generations, and that this influence is cumulative, increasing with the response of each successive generation. We also find that if, in the lifetime of a given individual, a particular stimulus is applied on two separate occasions with a certain interval between them, the response of that individual to the second application is generally brisker than its response to the first. By responding to the first application, the organism became attuned to that stimulus and enabled to respond more easily to it if it should be repeated, although the actual functional or structural modifications which constitute the response are purely temporary and pass away after a short time. But the attunement to the stimulus persists and it appears that this is the influence arising from the individual's response to the environment that can be transmitted in some degree to the following generations.

The actual adaptations themselves are not inherited. None of the experiments mentioned in this paper, excepting Durken's experiments with the pupae of *Pieris brassicae*, give any support to the idea that an actual functional or structural modification is directly inherited. It is an attunement to a stimulus that is transmitted, and even this attunement is not inherited in the geneticists' sense of the term, for all our available evidence shows that it is only inherited temporarily and that, if the stimulus concerned is lacking from the environment for a few generations, the attunement to the stimulus gradually fades.

In a recent paper McBride (1931) draws attention to the increased intensity of the response of successive generations to a new environment. He refers especially to the experiments of Durken, but he appears to think that this progressive increase in the response is evidence of the direct inheritance of an acquired character. Durken's experiments do indeed appear to lend some support to the idea of such a direct inheritance. But, as already pointed

out, his further researches proved that, even when the first generation showed no visible response to the orange-colored light, the second generation, when treated with the same light, produced nearly 100 per cent. of green pupae, and this makes it evident that in this case we are not dealing with the direct inheritance of an acquired character but with the inheritance of an attunement to a stimulus.

No suggestions are offered in this paper as to which exact parts of the germ cells act as the vehicle of this temporary heredity. We do not appear yet to be in a position to formulate any theory on this subject. Probably more harm than good has been done by efforts to devise mechanical systems which will enable us to understand how heredity is effected, before we are more fully acquainted with the actual facts of heredity. Both Weismann's and Rignano's theories are almost purely conjectural, and both of them may act as a hindrance to our ability to grasp the significance of new facts.

If the experiments and observations given in this paper can be regarded with some degree of confidence, it would appear to be very difficult to avoid the conclusion that an attunement to a stimulus can be inherited temporarily. Such a conclusion appears to throw some light on many questions. It serves to explain the contradictory and unsatisfactory results obtained in many experiments devised to prove the inheritance of acquired characters. For all workers have looked for the direct inheritance of an acquired character and this, it would appear, rarely or never occurs. They failed to notice that it is not the character itself that is inherited but the attunement of the organism to the stimulus that gave rise to that character.

Again this temporary heredity explains the immense value of a rich and varied racial experience. A race in sheltered and secure surroundings will become attuned to few stimuli, and if perchance suddenly exposed to some new danger can only react slowly and feebly. But a race exposed to varied surroundings and called on to contend with many enemies becomes attuned to many stimuli.

Few new dangers can catch it unawares. In the battle of life we see a survival of the alert. And may not the real value or at least one of the greatest values of bisexual reproduction be the enormous enlargement which it gives to the ancestral experience of the individual? Darwin (1859) pointed out that the inhabitants of small and isolated countries almost invariably go down before those of larger and unisolated ones, when the latter are introduced into their territory. The race with the richer and more varied ancestral experience wins.

A final question arises. Is the line of demarcation between temporary and permanent heredity an impassable barrier or do these two phenomena grade into each other? Mutations appear to be permanently inherited from their origin, and we have no evidence whatever of their gradual fading out, though natural selection may finally eliminate them. But can a character that arises in each generation on account of a deeply ingrained attunement to a stimulus become in time a permanently inherited character independent of any outside stimulus whatever? We can not definitely say. Many facts in nature would lead us to think that such a conversion is possible, but we have no unimpeachable proof. It may be that, after a character has arisen very early in the life history of countless generations, some particular event that has always coincided with or just preceded the application of the stimulus may itself become an effective stimulus to evoke the response. We know of many cases where obviously adaptive characters arise in the individual life history before there is any occasion for their exercise. The foetus of a Negro mother is heavily pigmented, although much lighter than the adult. Braus (1906) records an interesting example of a response continuing after the stimulus that apparently originally caused it was removed. Frog tadpoles grow their fore- and hind-limbs at the same time, but the fore-limbs are concealed for a period by the operculum of the gills, and when they are fully grown they rupture

the operculum and push their way out. Braus amputated the forelimbs before they had developed, and transplanted them under the skin of the back, where they developed. But in spite of the removal of the pressure due to the developing fore-limbs, the center of the operculum grew thin and transparent, and in some cases even broke down to form a hole, which was smaller, however, than that usually formed by the fore-limbs. Here a feature that apparently arose at first as a response to the pressure exerted by the developing fore-limbs continued to occur at least to some extent after the stimulus was removed.

Such a supposition would also explain Haeckel's fundamental biogenetic law that ontogeny repeats phylogeny. For as the attunement to a stimulus became more and more delicate in each successive generation the acquired character would arise earlier and earlier in the life history, until finally its appearance would pass over into the embryonic period and it would become a permanently inherited character. McBride (1924) in fact argues in the reverse direction that, if the law of recapitulation is true, new characters must arise earlier and earlier in the life of successive generations.

It seems therefore highly probable that in the course of time a character that originally arose in response to a definite stimulus in the environment of the individual will, owing to the continued action of the same stimulus, arise earlier and earlier in each succeeding generation, until finally it can be evoked by some internal stimulus that for many generations has coincided with the influence of the external and causative one.

SUMMARY

Experimental and observational evidence is cited, taken from many fields, and dealing with plants and animals both high and low in the evolutionary scale, which suggests the following conclusions:

(1) Acquired adaptive characters are always only temporary, even in the lifetime of the individuals in which

they have originated, unless they involve irreversible structural alterations, or unless the stimulus that produced them continues to act or has acted on many occasions and for some time.

(2) Although the acquired character is only temporary, the individual by responding to the stimulus that produced the character has become attuned to that stimulus, and this attunement to the stimulus endures much longer than the actual character itself, so that if the same stimulus is repeated the reaction of the individual to the second application is brisker than its reaction to the first.

(3) An attunement to a stimulus can be inherited in some degree and temporarily. Acquired adaptive characters therefore arise earlier and more easily in successive generations if the same stimulus continues to be applied.

(4) Acquired characters are rarely, if ever, directly inherited.

(5) It is suggested as a theory that possibly characters, which originally arose in response to an external stimulus in the environment, and in successive generations, arise earlier and earlier in the life history, owing to the inherited and progressively increased attunement of the organism to that stimulus, may finally be evoked by some internal stimulus that for many generations has coincided with the external causative one. The character would thus become permanently inherited.

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